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LES ORGANES GÉNITAUX MALES DES HÉMIPTÈRES NABIDAE. ABSENCE DE SYMBIONTES DANS CES ORGANES.

Par JACQUES CARAYON.

DANS une note récemment publiée ici-même (1949, *Proc. R. ent. Soc. Lond.* (A) **24** : 111–118) T. E. Woodward décrit les organes génitaux internes des mâles de quelques *Nabis*, et y signale la présence de microorganismes symbiotiques.

Cet auteur semble n'avoir pas peu connaissance de la note publiée sur ce sujet 5 ans auparavant (J. Carayon, 1945), note dans laquelle je décris les " éléments bacilliformes " observables dans les annexes génitales mâles de certains NABIDAE ; j'indique que ces éléments ne sont pas des Bactèries mais des produits complexes secrétés par les glandes annexes.

Cette opinion, opposée aux vues de T. E. Woodward, est basée sur l'étude anatomique et histologique de nombreux NABIDAE, appartenant aux sous-genres *Nabis*, *Dolichonabis*, *Himacerus*, *Stâlia*, *Aspilaspis* parmi les NABINAE, aux genres *Prostemma*, *Alloeorhynchus* et *Phorticus* parmi les PROSTEMMINAE.

Avant d'aborder la question des " éléments bacilliformes," une brève description des caractères généraux présentés par les organes génitaux internes des mâles de NABIDAE s'avère indispensable. Il sera utile de comparer ensuite ces caractères à ceux des mêmes organes chez les Hétéroptères de familles voisines.

CARACTÈRES ANATOMIQUES GÉNÉRAUX.

Les deux testicules comportent 7 lobes, enveloppés dans la membrane péritonéale, incolore ou pigmentée en rouge. De la base de chaque testicule part un canal déférent grêle, qui se renfle postèrieurement en une vésicule séminale plus ou moins individualisée. Les canaux déférents de chaque côté débouchent ventralement au sommet d'un bulbe éjaculateur impair, toujours bien développé. Le canal éjaculateur, qui prolonge postérieurement le bulbe, ne tarde pas à pénétrer dans l'organe copulateur par le foramen de la plaque basale.

Les glandes annexes principales sont toujours au nombre de deux paires :

Une paire de *mésadènies*, les plus antérieures, en forme de tubes assez régulièrement cylindriques et ramifiées, qui constituent deux buissons, et aboutissent dans deux *réservoirs mésadèniques* (" anterior reservoirs " ou " bacterial pouches " suivant T. E. Woodward) ; ceux-ci sont le plus souvent accolés, au moins en partie, à la paroi dorsale ou latérale des vésicules séminales ; ils pénétrent en même temps qu'elles, mais dorsalement, dans le bulbe éjaculateur.

Une paire d'*ectadènies*, qui sont également des glandes tubuleuses et ramifiées, mais beaucoup plus grêles que les mésadènies, et généralement variqueuses. Chez les NABINAE, ces glandes sont groupées en deux masses symètriques, à contour extérieur régulier, et qui entourent chacune plus ou moins complètement un réservoir central ; de ce réservoir part un canal efférent, qui se réunit avec celui du côté opposé, juste avant de déboucher dans la partie postérieure du bulbe éjaculateur, et au milieu de la face dorsale de ce dernier.

Aucun des NABIDAE examinés, n'est dépourvu de ces glandes ectadèniques, qui sont bien développées chez *Dolichonabis limbatus* (Dahlbom), (cf. fig. 1), contrairement à ce qu'indique et figure T. E. Woodward (1949, fig. 4).

Il existe en outre chez les NABINAE, un sac bilobé, à parois minces, qui entoure plus ou moins complètement la base du bulbe et le canal éjaculateur (*s*, fig. 1). Ce sac constitue sans doute une annexe de l'organe copulateur ; ses rapports anatomiques et son rôle restent à préciser.

STRUCTURE DU BULBE EJACULATEUR ET DES GLANDES ANNEXES.

(1) *Bulbe éjaculateur*.—Il comporte une partie antérieure mésodermique, de beaucoup la plus développée, et une partie postérieure ectodermique. L'ensemble est enveloppé d'une tunique conjonctive.

Le bulbe mésodermique, prolongement direct des vésicules séminales, a une épaisse paroi musculaire, en général progressivement amincie vers l'arrière ; cette paroi est tapissée intérieurement par un épithélium glandulaire, qui—chez les *Nabis*—constitue de plus une cloison transversale en forme d'entonnoir évasé, dont le tube est dirigé postérieurement. La cavité bulbaire mésodermique se trouve ainsi divisée en deux compartiments ; le compartiment antérieur est presque entièrement rempli par les fins et longs filaments rayonnants d'une sécrétion élaborée par les cellules glandulaires de la paroi. Ces cellules, dans le compartiment postérieur, présentent des caractères différents ; leur apex est creusé de vacuoles de plus en plus volumineuses, renfermant de gros grains de sécrétion. Les ensembles glandulaires du bulbe mésodermique doivent être considérés comme des *glandes annexes secondaires*.

Le bulbe ectodermique prolonge antérieurement le canal éjaculateur ; il a la forme d'une cupule à double paroi. Sa paroi externe, faite d'un épithélium simple, et dépourvue de couche musculaire, présente un diverticule médio-dorsal, origine des ectadènies ; celles-ci déversent par là leur sécrétion dans l'espace libre entre les deux parois. La paroi interne est étroitement accolée à la partie postérieure du bulbe mésodermique, qu'elle limite ; réduite en son milieu à l'intima chitineuse, elle constitue une seconde cloison transversale, encore en forme d'entonnoir, dont le tube se prolonge dans le canal éjaculateur.

Ce dispositif laisse libre un passage central pour le sperme et les sécrétions mésadèniques, mais parait empêcher le mélange de ces dernières avec la sécrétion ectadènique.

La structure du bulbe éjaculateur varie dans les détails, et semble présenter son maximum de complexité chez les NABINAE. La cavité de la portion mésodermique n'est pas divisée chez les PROSTEMMINAE, et il n'y existe qu'une seule catégorie de cellules glandulaires.

Le canal éjaculateur, avant son entrée dans l'organe copulateur, à un diamètre inférieur à celui du bulbe, mais présente des parois épaisses chez les *Nabis* ; en effet, des cellules glandulaires hautes et serrées tapissent ventralement ces parois, et dorsalement l'épithelium est pourvu d'une importante couche de chitine.

Au contraire, le canal éjaculateur des PROSTEMMINAE, au même niveau, possède des parois minces et presque transparentes, sans cellules glandulaires ; de ce fait, il apparait anatomiquement bien distinct du bulbe éjaculateur qu'il prolonge (voir fig. 2).

(2) *Mésadènies*.—Ces glandes comportent, sous une mince tunique conjonctive, une couche de cellules régulières, à peu près isodiamètriques, entourant une lumière centrale, plus ou moins encombrée par les granulations qu'

elles secrètent. Pourvues de noyaux ronds ou ovales, ces cellules ont un cytoplasme franchement basophile, très dense, et contenant de fines vacuoles. Des corpuscules de sécrétion se trouvent sur le bord interne des cellules et en rendent la limite imprécise.

Cette structure varie peu, non seulement parmi les NABIDAE, mais aussi chez les autres Hétéroptères, qui ont des mésadènies comparables.

(3) *Ectadènies.*—Sur les coupes histologiques, on distingue dans ces glandes, de l'extérieur vers l'intérieur : une fine membrane conjonctive, un épithèlium glandulaire à limites cellulaires peu nettes, avec des noyaux irréguliers et un cytoplasme granuleux, une intima chitineuse plus ou moins épaisse, qui borde une lumière assez réduite et vide. En effet, comme l'a indiqué T. E. Woodward (1949), la secrétion de ces glandes est un liquide huileux, assez volatil et odorant, que dissolvent complètement les réactifs histologiques.

Un caractère remarquable des ectadènies est l'abondance particulières des trachées, qui s'y ramifient.

La conformation et la structure de ces glandes sont plus variable que celles des mésadènies. Dans le genre *Phorticus* Stål, par exemple, les ectadènies sont constituées par deux tubes minces et longs, pelotonnés, et dont l'intima chitineuse est relativement épaisse.

DÉVELOPPEMENT.

Seules seront examinées ici les variations de dimensions, que subissent les différentes parties de l'appareil génital mâle, depuis la fin du stade nymphal jusqu'à la maturité sexuelle. Ces variations sont fort importantes.

Les testicules acquièrent leur développement maximum au cours du dernier stade larvaire, ou au début de la vie imaginale ; ils régressent ensuite ; la membrane qui les entoure se frippe, tandis qu'ils diminuent de volume ; leur forme peut alors se modifier de façon appréciable. Inversement, les annexes génitales se développement considérablement depuis la mue imaginale jusqu'à la maturité sexuelle.

Cette dernière, chez les mâles de tous les NABIDAE, que j'ai eu l'occasion d'étudier à cet égard, est acquise très rapidement, souvent quelques jours seulement après la mue imaginale. On observe un brusque accroissement corrélatif des annexes génitales, et notamment des réservoirs mésadèniques. Ceux-ci sont presque invisibles lors de l'éclosion imaginale, tandis que les glandes correspondantes sont déjà bien distinctes, mais ils acquièrent en peu de temps un volume souvent plusieurs fois supérieur à celui des testicules, en se remplissant des produits de l'intense activité secrétrice des mésadènies.

Il y a lieu de tenir compte de ces variations dans l'étude comparative des organes génitaux internes chez les différents genres ou espèces.

DIFFÉRENCES SPÉCIFIQUES OU GÉNÉRIQUES DE CONFORMATION.

Je me bornerai sur ce sujet à quelques brèves indications pour compléter, ou rectifier en partie, les données récemment fournies par T. E. Woodward (1949) à propos de quelques espèces du genre *Nabis* Latreille.

(1) *Sous-genres de Nabis.*—Deux espèces voisines, du même sous-genre, peuvent présenter d'appréciables différences des organes génitaux internes. Ainsi, *Himacerus apterus* (Fabricius), à maturité sexuelle, possède des ecta-

dènies très oblongues, et plus développées que chez aucun autre NABINAE ; ces glandes dépassent en avant les réservoirs mésadèniques, qu'elles masquent dorsalement. Elles sont, au contraire, chez *Himacerus lativentris* Boheman, au même stade, relativement petites et de forme différente.[1]

Des espèces appartenant à deux sous-genres, bien distincts à d'autres égards, ont parfois des appareils reproducteurs internes très comparables. Ainsi

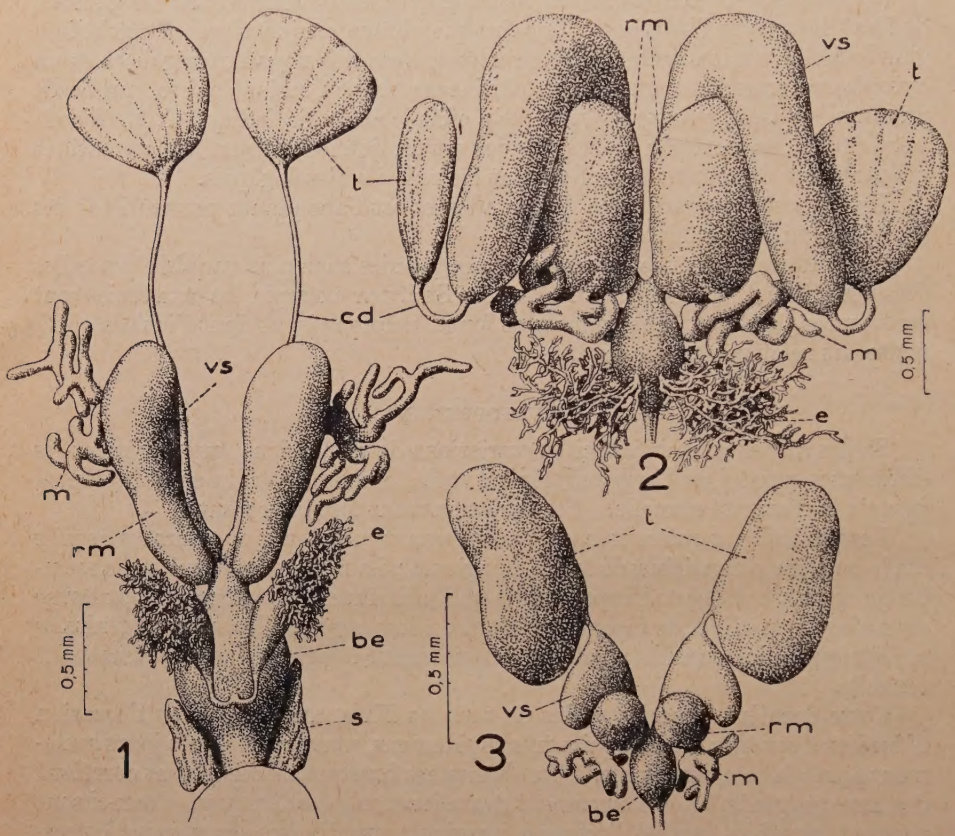

FIG. 1–3.—Organes génitaux mâles d'Hémiptères NABIDAE (1, 2) et ANTHOCORIDAE (3) ; vues dorsales. Chez : (1) *Dolichonabis limbatus* (Dahlbom), en août ; réservoir mésadènique gauche légèrement rabattu sur le côté pour monter la vésicule séminale correspondante. (2) *Prostemma guttula* (Fabricius), en septembre. (3) *Lyctocoris campestris* (Fabricius), en août. Les organes copulateurs et leurs annexes n'ont pas été figurés. *be.*, Bulbe éjaculateur ; *cd.*, canal déférent ; *e.*, ectadènie ; *m.*, mésadènie ; *rm.*, réservoir mésadènique ; *s.*, sac basal ; *t.*, testicule ; *vs.*, vésicule séminale.

Stâlia boops (Schiödte) et *Dolichonabis limbatus* (Dahlbom) possèdent des organes génitaux mâles présentant à peu près les mêmes particularités.

La fig. 1 montre les caractères de l'appareil reproducteur interne chez un mâle de *D. limbatus* à maturité sexuelle ; ces caractères ont été observés par

[1] *Nabis major* (Costa) appartient à mon avis au sous-genre *Stâlia* Reuter, et non au sous-genre *Himacerus* Wolff.

dissections de plusieurs specimens, et contrôlés sur coupes histologiques sériées. Plusieurs d'entre eux semblent avoir échappé à T. E. Woodward, qui a donné de cet appareil une description et une figure inexactes.

Je n'ai jamais observé dans cette espèce de testicules réniformes, mais peut-être ont-ils cet aspect chez de jeunes imagos. Les canaux déférents, lorsqu'ils atteignent le niveau des réservoirs mésadèniques, s'accolent étroitement à eux et se renflent légèrement en constituant deux vésicules séminales peu individualisées. Ces dernières et les réservoirs mésadèniques sont enveloppés dans une même membrane conjonctive, pigmentée en rouge orangé. Sur le vivant, réservoir et vésicule, formant de chaque côté une masse unique ("anterior pouch," suivant T. E. Woodward) peuvent être difficiles à distinguer l'un de l'autre ; cependant, après fixation, il est aisé de les voir et de les séparer à l'aide d'une fine aiguille. Sur la paroi des réservoirs mésadèniques, les vésicules séminales constituent deux cordons saillants et renflés à leur base.

Les différences de conformation entre les organes reproducteurs mâles des sous-genres de *Nabis* sont en général faibles ; elles portent sur les vésicules séminales, (nettement individualisées chez les espèces des S. G. *Nabis* Latreille et *Aspilaspis* Stål, mais peu différenciées dans les autres sous-genres) sur le point où aboutissent les mésadènies dans leurs réservoirs, sur la forme et le développement relatif des ectadènies.

(2) Prostemminae.—Leurs organes génitaux mâles sont beaucoup plus variables. La fig. 2 en montre l'aspect chez *Prostemma guttula* (Fabricius). La conformation si particulière des vésicules séminales diffère déjà beaucoup dans d'autres espèces du même genre ; et par exemple, chez *P. eva* Kirkaldy d'Afrique tropicale, ces organes présentent une forme en S. Dans plusieurs espèces des genres *Alloeorhynchus* Fieber et *Phorticus* Stål, les vésicules séminales, toujours nettement différenciées, rappellent celles de certains *Nabis* par leur forme non incurvée, mais sont globuleuses.

Prostemminae et Nabinae diffèrent beaucoup par la conformation du bulbe éjaculateur et des ectadènies. Ces dernières, dans les genres *Prostemma* et *Alloeorhynchus* forment une masse diffuse entourant presque complètement le canal éjaculateur et le bulbe ; elles n'ont pas de réservoirs comparables à ceux de ces glandes chez les *Nabis* ; leur sécrétion semble s'accumuler dans une vaste poche impaire, à paroi mince et plissée, qui débouche dorsalement dans la cavité logeant l'organe copulateur ; le liquide huileux contenu dans cette poche se répand à l'extérieur, lors de l'accouplement en dégageant une odeur pénétrante. Il existe en outre deux gros tubes contournés, insérés par leur milieu dans deux orifices à la base de l'organe copulateur, et qui paraissent d'autre part en rapport avec les ectadènies. Des investigations ultérieures sont nécessaires pour préciser les relations anatomiques et le rôle de ces annexes, particulières aux Prostemminae, et qui n'ont pas été représentées fig. 2, non plus que le vaste réservoir impair signalé plus haut.

Comparaison avec les Organes Génitaux Males des Hétéroptères des Familles Voisines.

Si l'étude comparative des organes génitaux internes présente peu d'intérêt pour juger des affinités ou des différences entre espèces ou sous-genres, son importance à cet égard s'accroît avec les groupements considérés, et devient primordiale à l'échelle des Familles.

Ainsi, les NABIDAE sont généralement considérés comme très voisins des REDUVIIDAE, mais les caractères généraux de l'appareil reproducteur interne de ces Hétéroptères diffèrent considérablement (cf. J. Carayon, 1944). Par contre, on constate aisément en comparant l'appareil reproducteur mâle des NABIDAE et celui décrit chez *Cimex lectularius* L., entre autres par L. Dufour (1833) et L. Landois (1869), que ces appareils sont très voisins, comme je l'ai déjà signalé à plusieurs reprises (J. Carayon, 1945, 1946). La même conformation générale s'observe chez les ANTHOCORIDAE, dont l'étroite parenté avec les CIMICIDAE est connue avec certitude depuis longtemps.

La fig. 3 montre les caractères des organes reproducteurs mâles de *Lyctocoris campestris* (Fabricius), comme exemple de la conformation de ces organes chez les ANTHOCORIDAE. La seule différence entre l'appareil génital mâle des NABIDAE d'une part, celui des CIMICIDAE et ANTHOCORIDAE d'autre part est l'absence chez ces derniers des ectadènies constamment présentes chez les premiers.

Il est important de noter pour le sujet qui nous occupe que CIMICIDAE et ANTHOCORIDAE possèdent des mésadènies et des réservoirs mésadèniques semblables, tant par leur conformation que par leur structure à ceux des NABIDAE.

Bien d'autres caractères anatomiques comparables, s'ajoutant aux similitudes des organes génitaux, confirment l'opinion exprimée par O. M. Reuter en 1908, et prouvent les grandes affinités qui rapprochent NABIDAE, ANTHOCORIDAE et CIMICIDAE. D'aussi nombreuses différences démontrent que, malgrè certaines convergences d'aspect extérieur, REDUVIIDAE et NABIDAE n'ont qu'une parenté très lointaine.

PRODUITS DE SECRETION DES MÉSADÈNIES ET CONTENU DES RÉSERVOIRS MÉSADÈNIQUES.

Puisque des mésadènies et des réservoirs mésadèniques (" Bacterial pouches" de T. E. Woodward) semblables existent, non seulement chez les *Nabis*, mais aussi chez tous les NABIDAE, ANTHOCORIDAE et CIMICIDAE, il importe de faire un examen comparatif du contenu de ces organes chez de nombreux représentants de ces différents Hétéroptères.

Cet examen permet de constater que les réservoirs mésadèniques contiennent très généralement, chez les individus à maturité sexuelle :

(1) Une substance fluide ou semi-fluide, le plus souvent incolore, parfois teintée légèrement en jaune ou en vert ; cette substance est coagulée par les fixateurs histologiques, soit en larges flaques, sans structure ou très finement granuleuses, soit en réseaux. On retrouve cette substance dans certaines parties de la lumière des mésadènies, mais de façon très inconstante, ce qui porte à croire qu'elle n'est pas produite par ces glandes, mais plus probablement par l'épithèlium des parois des réservoirs.

(2) Des corpuscules de consistance solide en apparence, dont les dimensions et les formes sont extrêmement variables. *In vivo*, ils sont le plus souvent incolores, transparents et fortement réfringents. Les colorants histologiques les teintent différamment de la substance précédente, dans laquelle ils baignent.

Chez un petit nombre d'espèces de *Nabis*, et notamment *N. ericetorum* Scholtz et *N. ferus* (Linné), ces corpuscules présentent un curieux aspect bacilli-

forme, et leurs amas très denses évoquent une population de microorganismes. Comme je l'ai précédemment indiqué (J. Carayon, 1945), cette impression est encore augmentée par l'aspect fréquemment hétérogène de la substance qui constitue ces corps bactèroïdes. On y observe des vacuoles plus ou moins nombreuses, et souvent une auréole périphèrique plus claire que le centre.

Bien que T. E. Woodward n'ait donné aucun caractère précis, aucune dimension ni aucune figure des Symbiontes, qu'il dit avoir observé, tout me porte à croire que ce sont ces éléments bacilliformes, qu'il a considérés comme des microorganismes. En tout cas, il n'existe pas dans les réservoirs mésadèniques d'autres corpuscules, ayant une apparence bactérienne.

Même chez les espèces, où ils présentent un aspect bacilliforme marqué, ces éléments surprennent par la variabilité de leur forme et de leur taille, qui va de 5 à 80μ environ. Aucun des microorganismes connus comme associés à des Hétéroptères n'atteint ces dimensions et ce polymorphisme, qui ne pourraient être comparés qu'à ceux des Symbiontes très spécialisés de certains Homoptères. Dans de nombreuses espèces de NABIDAE (*Himacerus lativentris*, *Dolichonabis limbatus*, *Aspilaspis viridulus*, *Nabis capsiformis*, *Alloeorhynchus flavipes*, *Phorticus flavus*, par exemple) et d'ANTHOCORIDAE (différentes espèces d'*Anthocoris*), les corpuscules n'offrent plus aucun aspect bactèroïde ; ils sont ovoïdes ou plus souvent sphèriques, et leurs dimensions sont toujours très variables.

Chez *Cimex lectularius*, L. Landois, en 1869, a décrit et figuré avec précision (Planche xviii, fig. 7) les corpuscules ovoïdes ou en forme de courts bâtonnets, que l'on trouve dans les mésadènies et dans leurs réservoirs, contenant aussi une substance liquide. Il ne parait pas douteux que ces corpuscules, faits d'une matière très réfringente, soient homologues de ceux des *Nabis*. Or, les CIMICIDAE, Hétéroptères strictement hémophages, possèdent des Symbiontes authentiques, logés dans un mycétome, et dont P. Buchner (1923) a décrit la transmission par envahissement des ovocytes, au cours de l'ovogénèse. Dans ces conditions, il serait parfaitement illogique de considérer comme des Bactèries, les éléments contenus dans les mésadènies, éléments qui n'ont aucun point de ressemblance avec les véritables Symbiontes.

Dans quelques cas enfin, notamment chez *Prostemma guttula* et chez *Lyctocoris campestris*, les corpuscules se présentent comme de véritables gouttelettes, d'une substance non miscible au liquide environnant. Ces gouttelettes, après fixation et coloration ne se teintent pas elles-mêmes, mais contiennent un réseau irrègulier, qui retient les colorants ; elles sont parfois confluantes en une masse, qui occupe une part importante du réservoir (*Lyctocoris*).

Ces corpuscules mésadèniques sont sans doute formés d'une substance complexe lipoprotéique, dont l'hétérogénéité d'aspect rappelle ce que l'on observe parfois dans des boules de vitellus par exemple.

Les mésadènies secrètent de fins granules, suivant un processus comparable à celui de la sécrétion mésentèrique, ainsi que A. Berlese l'indiquait dès 1898, pour les mésadènies de *Graphosoma lineatum* (L). Ces granules, d'après T. E. Woodward, seraient mélangés avec les Symbiontes, qui s'en nourriraient. Malheureusement, pour cette hypothèse, on trouve, dans la lumière des mésadènies, tous les intermédiaires entre les plus fins granules de sécrétion et les plus gros des pseudosymbiontes. Les examens histologiques montrent de nettes images d'agglomération progressive des granules, qui le plus souvent se colorent

tous de la même façon, quelle que soit leur taille. Il arrive (chez *Dolichonabis limbatus* par exemple) que les plus grands corpuscules soient brûnâtres, alors que les petits se teintent en rose par l'éosine ; mais là encore on observe aisément tous les intermédiaires de coloration, et il est probable qu'il se produit une transformation chimique légère après la sécrétion des corpuscules.

Le Devenir des Sécrétions Mesadèniques dans les Organes Génitaux des Femelles.

A. Berlese a signalé en 1898, que chez *Graphosoma lineatum* (L.), les granules secrétés par les mésadènies sont injectés en grande abondance au cours de l'accouplement, dans les voies génitales des femelles, où on les trouve mélangés avec les spermatozoïdes. En 1945, j'ai indiqué le même fait chez les *Nabis* ; corpuscules mésadèniques et spermatozoïdes sont principalement accumulés à la base des oviductes ; on les observe aussi contre la paroi de la chambre génitale et dans des anfractuosités, provoquées dans cette paroi de chitine très molle par le pénis du mâle.

Chez tous les Nabidae, hivernant à l'état imaginal, la fécondation est effectuée dès la fin de l'été, donc bien avant la période de ponte, qui commence au printemps suivant. Si les spermatozoïdes peuvent subsister de longs mois dans l'organisme des femelles, où on les trouve chez la plupart des specimens récoltés pendant l'hiver, il n'en va pas de même des corpuscules mésadèniques. Quelque temps après la fécondation, les coupes histologiques du tractus génital des femelles montrent par endroits ces corpuscules encore reconnaissables, mais agglomérés les uns aux autres, très déformés et plus ou moins diffluants ; plus tard il n'y en à aucune trace, et il est fréquent que l'appareil génital de femelles prêtes à pondre en soit totalement dépourvu.

Absence de Symbiontes chez les Nabidae.

M. Kuskop (1920) et G. Schneider (1940), tous deux spécialistes avertis des questions de symbiose chez les Hémiptères, indiquent avoir recherché en vain des Bactèries symbiotiques chez les Nabidae. Cependant, T. E. Woodward (1949) prétend retrouver en abondance dans les testicules et dans le tube digestif des *Nabis* des éléments bactériens semblables à ceux qu'il décrit comme tels dans les réservoirs mésadèniques. Au cours de l'examen de nombreux specimens de divers Nabidae, je n'ai jamais constaté la présence constante de Bactèries dans ces organes, et je n'y ai jamais observé de corpuscules comparables à ceux des mésadènies. Cependent ces corpuscules sont généralement aisément repérables sur coupes histologiques, grâce à la teinte particulière que leur confèrent les colorants.

On peut noter seulement la présence assez fréquente dans le tube digestif de Protozoaires parasites : Grégarines ou Flagellés, et de Bactèries de type banal. Ces dernières, dont la présence n'est pas constante, et qui sont souvent peu nombreuses, n'ont pas les caractères de Symbiontes.

Avec M. Kuskop et G. Schneider, je considère donc les Nabidae comme dépourvus de véritables microorganismes symbiotiques. Ceci est en accord avec l'absence très générale de Symbiose chez les Insectes prédateurs.

On sait que, chez les Hémiptères, le régime alimentaire parait conditionner de façon particulièrement nette l'existence de la Symbiose. Par exemple,

les Asopinae, prédateurs, et non suceurs de sève comme les autres Pentatomidae, sont les seuls membres de cette famille, qui soient privés de Symbiontes. Inversement, il n'y a pas de microorganismes symbiotiques chez les Reduviidae prédateurs, mais les quelques formes hémophages telles que *Rhodnius* et *Triatoma* en sont pourvues.

Chez les mâles d'un Pentatomidé, possèdant d'authentiques Symbiontes, *Nezara viridula* L., N. S. R. Malouf à signalé en 1933 la présence de microorganismes, identiques à ceux des cryptes bactèriennes intestinales, dans deux réservoirs des annexes génitales. D'après cet auteur, les Symbiontes contenus dans les réservoirs, injectés en même temps que le sperme dans les voies génitales des femelles, serviraient à infester les oeufs au moment de la ponte.

T. E. Woodward voyant dans cette observation un cas analogue à ce qu'il croit observer chez les *Nabis*, suggère non seulement que le même mode de transmission existe chez ces derniers, mais qu'il est probablement assez général parmi les Pentatomidés.

J'ai précédemment indiqué (J. Carayon, 1945) que l'observation de Malouf est probablement inexacte, peut-être par suite d'une confusion entre les véritables Symbiontes et les corpuscules secrétés par les mésadènies.

Chez les Hétéroptères pourvus, comme *N. viridula*, de cryptes bactèriennes en communication avec la lumière du tube digestif (Pentatominae, Plataspidae, certains Lygeidae, etc.) il parait en effet nettement établi que les femelles utilisent, pour contaminer leurs oeufs, *les Symbiontes provenant de leur propre tube digestif*. Les cryptes bactèriennes de ce dernier sont toujours plus développées que celles du tube digestif des mâles ; elles sont particulièrement gonflées par d'abondants Symbiontes pendant la période de ponte ; fréquemment, les plus postérieures d'entre elles se renflent en un " organe de transmission," bourré de Bactèries un peu différentes des Symbiontes habituels (formes de contamination). Ces Bactèries gagnent l'intestin postérieur, et, mêlées à une secrétion du tube digestif, constituent l'enduit, qui sort par l'orifice anal pendant la ponte, et que les femelles déposent sur leurs oeufs.

Ces faits ont été établis notamment par les travaux de W. Rosenkranz (1939) et de G. Schneider (1940) ; observés chez des Hétéroptères très voisins de *Nezara viridula*, ils rendent difficilement plausible l'existence chez cette espèce d'un mode de transmission aussi particulier, que celui indiqué par Malouf.

Summary.

The general anatomical characters of the reproductive system in males of Hemiptera Nabidae are described. In all the species studied, in Nabinae as well as in Prostemminae, at least two pairs of accessory glands, generally branched, open in the bulbus ejaculatorius : anterior mesadenia with their receptacles, and posterior ectadenia.

In the subgenus *Dolichonabis*, the ectadenia are present, and mesadenial receptacles, tightly jointed to seminal vesicles, are clearly distinct from the latter, as in the other sub-genera of *Nabis*.

Some points in the histological structure of reproductive organs are described, especially for bulbus ejaculatorius, mesadenia and ectadenia.

The differences of conformations of the reproductive system among the subgenera of *Nabis* are generally minute, and sometimes without any con-

nection with taxonomic divisions. Those differences are more marked between genera of PROSTEMMINAE. The latter differ mainly from NABINAE in the structure of their ectadenia and bulbus ejaculatorius.

The main point of interest presented by the internal organs in NABIDAE is to prove quite clearly that this family diverges strongly from REDUVIIDAE, and offers the greatest affinities with CIMICIDAE and ANTHOCORIDAE.

The symbiotic Bacteria, recently described inside the mesadenial receptacles of some *Nabis*, are nothing more than bodies secreted by the mesadenia. Various proofs are given of this fact, particularly demonstrated by comparative histological studies of mesadenial glands and receptacles, together with their content, in numerous species of NABIDAE, ANTHOCORIDAE and CIMICIDAE.

No group of predatory insects is at present known as associated with symbiotic bacteria. In accordance with this fact, the Hemiptera NABIDAE seems to be entirely devoid of actual symbionts.

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SOME OBSERVATIONS ON THE BIOLOGY OF THE AUSTRALIAN WASP *POLISTES HUMILIS* FABR. (HYMENOPTERA : VESPIDAE) IN NORTH AUCKLAND (NEW ZEALAND), WITH SPECIAL REFERENCE TO THE NATURE OF THE WORKER CASTE.

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In June, 1948, during a visit to the far north of New Zealand, the opportunity was taken to make observations on *Polistes humilis* at the mid-winter period. At this time, adults of both sexes were found overwintering in clusters on nests in which brood rearing had ceased. The nests, together with the adults present, were taken for subsequent analysis.

During the period December, 1948, to March, 1949, further observations were made on nests of various sizes during the active brood-rearing season.

While the extent of this work is limited, it is hoped that some information contained herein may be of interest. Little statistical analysis of populations in the nests of European species has been made, and the nature of worker-queen relationships is by no means thoroughly understood.

In the present work an attempt has been made to discover the nature of the worker-queen complex by studying the size, the ovarial development and the extent of fertilization of females present on nests. Notes on the biology and an account of an extremely large nest are also presented.

1. General.

Polistes humilis has been present in New Zealand for many years. Its spread has been governed by climatic conditions. Only north of Auckland do these wasps become very plentiful, and their abundance in any one area varies noticeably from year to year.

Nests are constructed of typical wasp paper consisting of masticated wood cemented together with saliva and propolis. The shape of nests is extremely variable and the size ranges from 20 or 30 to well over 1000 cells. The nests are always suspended by a single stalk, which is darker and well reinforced with resinous substances.

Nests occur in a wide variety of places. Some are attached to posts and fences, or hang in low-growing or high sheltered bushes and hedges. They are commonly found in sheltered positions on the outside of buildings. Another favoured place is the *Phormium* bushes which grow in low, damp areas. Here the wasps build on the lower side of blades which have arched over and provide adequate protection from rain. The size of the nest is in part limited by the nature of the object to which it is attached and in part by the fact that the habit of multiple supports has not been developed. In large nests the weight of the brood may be considerable and where peripheral sections are showing signs of collapse there is no attempt to provide new support, but only a re-alignment to the new angle in cells being constructed. The question of the number of adults concerned in the founding of the nest is, of course, an additional factor in determining the size of nests.

Where nests are built in the open they are usually bell-shaped, but when they are constructed adjacent to walls this symmetry is lost and they become elongated.

Nests may be newly founded each year, or they may become extended during the second year. Several females may join a newly founded nest. In the case of a nest extending into a second year, a large number of females which presumably have wintered on the nest, may commence brood rearing and extension of the nest during spring. A newly founded nest may contain as many as 400 cells by the end of the first year, but the majority do not reach this size. Most nests are annual developments.

During the warmer months the female wasps will be seen searching clumsily amongst the foliage for caterpillars, which they malaxate and feed to the larvae in the nest. The males will be noticed flying swiftly up and down the taller foliage, searching for the females.

In the cool of evening or during cold periods the wasps do not leave the nests, for they are unable to fly. In winter, too, they are unable to leave the hibernating clusters on the nests except during unusually warm weather. When temperature thus limits their activity individuals are easily handled with fine forceps. The summer nests were taken on cooler evenings, which, in addition to ensuring that most of the individuals were home, facilitated their handling.

The wasps are not aggressive unless the nest is disturbed. They probably aid in reducing the numbers of caterpillars on some agricultural crops. Any clearing of scrub where nests are plentiful invariably becomes a winter procedure.

2. Data from the Summer Nests.

Nests 1–14 were taken at Paihia, Bay of Islands, nest 15 from Kaikohe, which is inland. Table I shows the wing length (mm.) of adult females from nests, those taken with the nest being shown separately from those which subsequently hatched or were dissected out from the nest. In measuring the wing length the distance from the centre of the tegula to the tip of the wing was taken to the nearest half-millimetre.

It will be noted that the curves are unimodal, indicating that the female individuals of a nest do not fall into two distinct size groups. Any increase in average size of the individuals in the nest would appear to be correlated with the size of the nest rather than with the date the nest was taken. No long seasonal cycle is necessary before individuals of the size which are going to perpetuate the species are produced. It is interesting to note that in the extremely large nest (No. 2) the "subsequently hatched" are noticeably smaller on the average, possibly indicating a less successful condition for larval nutrition. In Nest 1, from the same verandah ledge and a few feet distant, the subsequently hatched are noticeably larger. No. 1 was a newly founded nest. No 2 was observed in the previous June, when it consisted of about 400 cells and a large cluster of adults hibernating above it.

Table II provides nest and brood data.

Dissections of all female adults taken with the nests were made to gain information on ovarial development and fertilization. Table III provides data on ovarial development, and Table IV summarizes the information on fertilization. In Table III the number of eggs refers to the total of the eggs in all the ovarioles, which are larger than nurse cell groups immediately preceding them (Cumber, 1948). In Table IV the presence or absence of sperm was checked microscopically. It will be noted that ovarial development and fertilization are not restricted to larger individuals but may occur throughout the whole size range.

TABLE I.—*Wing Length (mm.) of Adult Females.*

Number of nest.	Date taken.	Total females taken with nest.*	Wing length. 10·75	11·25.	11·75.	12·25.	12·75.	13·25.	13·75.
		A. *Taken with nest.*							
1	11.i.49	12	.	.	2	3	1	5	.
2	11.i.49	214	.	2	19	35	54	75	3
3	21.ii.49	3	.	1	1	.	.	1	.
4	24.ii.49	3	.	.	1	1	.	.	.
5	1.iii.49	4	.	.	.	2	.	.	1
6	3.iii.49	13	.	2	1	5	3	.	1
7	13.iii.49	1	.	.	1	.	.	.	.
8	13.iii.49	2	.	.	1	1	.	.	.
10	19.iii.49	4	.	1	2	1	.	.	.
11	19.iii.49	4	.	.	1	1	2	.	.
12	20.iii.49	5	1	1	.	1	1	1	.
13	23.iii.49	4	2	.	1	1	.	.	.
14	26.iii.49	16	.	.	4	5	6	1	.
15	1.iv.49	47	.	.	.	2	13	29	3
		B. *Subsequently hatched and/or dissected out from nest.*							
1	11.i.49	12	.	.	.	.	3	10	3
2	11.i.49	214	2	7	40	85	68	16	.
4	24.ii.49	3	.	.	.	.	.	.	1
5	1.iii.49	4	.	.	.	.	1	.	.
15	1.iv.49	47	.	.	.	.	.	7	5

* Wear of wing tips prevented measurement of some individuals.

TABLE II.—*Nest and Brood Data.*

Number of nest.	Date nest taken.	Adults present. Males.	Females.	Adults obtained from brood. Males.	Females.	Total cells in nest.	Cells spun over.	Number broodless cells.	Total eggs in cells.	Larvae by instars. 1.	2.	3.	4.	Pupal brood.† Males.	Females
1	11.i.49	2	12	8	16	146	27	.	62	16	8	17	15	.	.
2	11.i.49	239	214	170	218	1290	398	.	802	96	46	77	274	.	.
3	21.ii.49	.	3	.	.	44	0	1	10	4	2	3	2	.	.
4*	24.ii.49	6	3	4	2	53	13	.	14	7	5	5	9	?	?
5	1.iii.49	.	4	8	1	32	13	.	2	2	4	2	9	.	1
6*	3.iii.49	2	13	9	.	70	17	.	18	7	7	4	17	?	?
7	13.iii.49	.	1	2	.	10	2	.	3	3	.	.	2	.	.
8	13.iii.49	.	2	2	.	14	4	4	.	.	.	4	2	2	.
10	19.iii.49	.	4	.	.	24	5	8	2	2	3	.	4	4	.
11	19.iii.49	2	4	1	1	40	2	28	.	.	1	.	3	.	.
12	20.iii.49	1	5	.	.	34	10	.	12	4	2	2	4	6	4
13	23.iii.49	1	4	4	.	36	6	.	9	4	3	5	9	2	.
14*	26.iii.49	20	16	?	?	113	36	11	3	7	13	20	23	?	?
15	1.iv.49	75	47	13	12	201	95	84	7	4	4	3	4	0	68

* Brood destroyed by mice before pupal brood analysis.
† No prepupal brood was present due to time between nest-taking and dissection out of spun-over brood. Nests 1–14. from Paihia, Bay of Islands; Nest 15 from inland area, Kaikohe.

TABLE III.—*Ovarial Development of Females from Nests.*

Number of nest.	Date nest taken.	Total females with nest.	Number of females dissected.	Number with countable eggs.	Average number eggs per developed female.	Range in number of eggs.	Number females showing ovarial slight filling.	Wing length (mm.) of females* with countable eggs. 10·75.	11·25.	11·75.	12·25.	12·75.	13·25.	13·75.
1	11.i.48	12	12	5	16·8	4–37	1	.	.	.	1	1	3	.
2	11.i.48	214	214	87	36·8	1–48	2	.	1	4	10	25	74	.
3	21.ii.48	3	3	1	5	.	.	.	.	.	.	.	1	.
4	24.ii.48	3	3	1	12	.	.	.	.	.	.	.	.	.
5	1.iii.48	4	4	1	12	.	.	.	.	.	.	.	.	.
6	3.iii.48	13	13	1	17	.	.	.	.	.	.	.	.	1
7	13.iii.48	1	1	.	.	.	.	.	.	.	.	.	.	.
8	13.iii.48	2	2	.	.	.	.	.	.	.	.	.	.	.
10	19.iii.48	4	4	.	.	.	.	.	.	.	.	.	.	.
11	19.iii.48	4	4	.	.	.	.	.	.	.	.	.	.	.
12	20.iii.48	5	5	1	15	.	.	.	.	.	.	.	1	.
13	23.iii.48	4	4	1	4	.	.	1	.	.	.	.	.	.
14	26.iii.48	16	16	.	.	.	.	.	.	.	.	.	.	.
15	1.iv.48	47	47	1	2	.	4	.	.	.	.	1	.	.

* Where this could be measured accurately.

TABLE IV.—*Fertilized Females in Nests.*

Number of nest.	Date nest taken.	Total females with nest.	Number females examined.	Number fertilized.	Wing length (mm.) of fertilized females.						
					10·75.	11·25.	11·75.	12·25.	12·75.	13·25.	13·75.
6	3.iii.49	13	13	1	.	.	.	.	.	.	1
8	13.iii.49	2	2	1	.	.	.	1	.	.	.
10	19.iii.49	4	4	2	1	.	1	.	.	.	.
12	20.iii.49	5	5	5	1	1	.	1	1	1	.
13	23.iii.49	4	4	1	1	.	.	.	.	.	.
14	26.iii.49	16	16	.	.	.	3	.	2	.	.
15	1.iv.49	47	47	22	.	.	.	.	6	13	3

3. DATA FROM NESTS AT MID-WINTER.

Table V shows the wing length of females from clusters of wasps taken on nests from a flax swamp at Kaikohe on 28.vi.48. The number of males in these clusters and the number of cells in the nests are also indicated. The adult data were obtained from material preserved in alcohol and the determination of fertilization was not possible.

TABLE V.—*Data from Nests Taken at Kaikohe on* 28.vi.48.

Number of nest.	Number of cells.	Total adults.		Wing length (mm.) of females.						
		Males.	Females.	11·25	11·75.	12·25.	12·75.	13·25.	13·75.	14·25.
1	144	5	9	.	.	.	1	4	4	.
2	262	27	121	1	1	9	23	51	34	2
3	164	2	20	.	.	3	4	9	4	.
4	103	12	11	.	3	.	.	4	3	1
5	184	44	157	1	3	23	39	54	36	1
6	154	8	28	.	.	2	10	13	3	.
7	147	14	155	.	1	8	35	68	43	.
8	140	10	70	.	.	4	14	30	22	.
9	120	12	89	1	3	5	16	39	23	2

4. A PARTICULARLY LARGE NEST FROM PAIHIA, BAY OF ISLANDS.

In June, 1948, a large nest of *Polistes humilis* was observed hanging beneath the verandah ledge of a house at Paihia. The nest was estimated to consist of about 400 cells. No brood was present in the nest and about 200 males and females formed a cluster around the stalk between the top of the nest and the ledge to which it was attached.

In January, 1949, the nest was again visited. By this time it had extended very considerably (Nest No. 2). The nest was no longer circular, but had extended laterally along under the ledge. By this time it consisted of well over 1000 cells and more than 400 adults were present. A large amount of brood in all stages of development made the nest quite heavy. There was still only the one central stalk, which had been considerably reinforced. Consequently the extremities of the nest were beginning to sag and newly formed cells were re-aligned to this. When the nest was taken on 11.i.49 it was 29 cm. in length and 11 cm. in width at the widest part.

The nest was taken at dusk, when it was possible to remove wasps individually with forceps and without undue disturbance.

After the brood from the open cells had been analysed and removed, the nest was kept until all the spun-over brood had emerged. The adults were removed from the nest from time to time, their wing length (mm.) being recorded. Table VI gives a record of the dates and the size of female adults emerging subsequent to taking the nest. The numbers of males emerging are also recorded.

TABLE VI.—*Emergences from Nest* 2.

Date of emergence.	Total adults emerging.		Wing length (mm.) of females.							Average wing length, females.
	Males.	Females.	10·75.	11·25.	11·75.	12·25.	12·75.	13·25.	13·75.	
11.i–16.i.49	35	22	1	1	4	6	7	3	.	12·38
17.i–22.i.49	43	17	.	.	3	8	5	1	.	12·40
23.i–29.i.49	32	38	.	2	9	18	6	3	.	12·26
30.i–5.ii.49	56	64	.	1	13	22	23	5	.	12.42
6.ii–11.ii.49	43	40	.	.	6	16	17	1	.	12·37
12.ii–17.ii.49	26	37	1	3	5	15	10	3	.	12·28

5. DISCUSSION.

In social Hymenoptera we may recognize three different degrees in the development of the worker caste.

(*a*) The worker and queen are morphologically separate. In this category belong the APIDAE and MELIPONINAE.

(*b*) The worker and queen, although having no morphological differences, show marked differences in size, as in some BOMBIDAE.

(*c*) The worker and queen have no morphological differences, nor do they fall into two distinct size groups. This appears to be the position in some species of *Polistes* and *Mischocyttarus* (Richards, 1945).

No morphological differences have been observed by which the female individuals from a nest of *Polistes* may be divided into two categories, and it is unlikely that this occurs. Measurements submitted in this paper have shown that female individuals do not conform to two distinct size groups. Moreover, it has been shown that females of all sizes may be fertilized and may develop their ovaries. The conception of a worker caste would appear to develop into one of relationship of individuals of a continuous size range. Pardi (1942, 1946) has studied the psychological relationship of individuals in nests of *Polistes*. He is concerned, however, mainly with the question of domination rather than with the nature of the worker caste.

Males are present at all times, and the females of all sizes are capable of fertilization.

It is obvious from the study of nests that some females do function as workers so long as the domination by another or other females occurs. In small nests founded by a single female the first one or two females produced are usually small and function as workers. These may or may not be fertilized, but they remain as workers until the original larger and dominating female leaves the nest. But under these circumstances this loss of the foundress does not necessarily mean that the nest will die out after a short period of male production.

Among those females which overwinter is a proportion of smaller individuals which are presumably fertilized. In the founding of nests during the spring, no doubt many of these females will become the " auxiliary queens " (Pardi) where several overwintering females occupy the one nest. But unless the dominating female leaves the nest these " auxiliaries " will function as workers, although they have overwintered, are fertilized and are themselves capable of founding a colony.

Richards (comm.) has suggested that although the female individuals from the one nest do not fall into two size groups, if from several nests all the females with developed ovaries are picked out, they may tend to have a larger average size than those with undeveloped ovaries. This is probably so in *P. humilis*. The separate analysis of nests known to be annual and biennial would prove interesting, as there might be relatively more nest construction work in annual nests.

6. Summary.

1. The populations of wasps on nests of *P. humilis* at midwinter have been analysed.

2. Nests have been studied during the active brood-rearing season, and brood and adult wasps have been analysed.

3. A particularly large biennial nest is described.

4. The nature of the worker caste in relation to other social Hymenoptera is briefly discussed.

7. References.

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APHIDS CAPTURED IN A ROTHAMSTED SUCTION TRAP, 5 FT. ABOVE GROUND LEVEL, FROM JUNE TO NOVEMBER, 1947.

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1. Introduction.

The quality and quantity of aphid populations at high altitudes depends primarily on the populations flying a few feet above ground level. A study of aphids at a low level was therefore undertaken as part of a larger programme on aphid drift. This paper deals with the species caught during the first season ; an analysis of ecological factors is not made here.

A suction trap was used ; this sucked in air at a constant rate of approximately 116,000 cu. ft./hr. in all wind-speeds of entomological significance. Its catches were therefore more direct indices of aphid density than those from tow-nets or sticky traps whose catching power varies with changing wind-speed. Suction trap records for any period can thus be more safely compared without employing the correction for wind-speed necessary with tow-nets (Hardy and Milne, 1938 ; Freeman, 1945). The relative proportions of species are also likely to be more accurate than with data from tow-nets and sticky traps (Johnson, 1950*b*).

2. Methods.

The trap was a prototype of a more carefully devised apparatus (Johnson, 1950*a* and *b*) and was situated at the edge of Great Field II, a pasture, near the meteorological enclosure, Rothamsted Experimental Station, at Harpenden, about 25 miles north of London. It consisted of a powerful electric fan, 18 in. in diameter, sucking air through a muslin cone suspended in the top of a vertical duct, which was 5 ft. above ground level. The air speed through the intake was sufficiently high for winds up to 10 m.p.h. past the trap to have a negligible effect on the rate of air sampled. Meteorological records were taken once a day at 10.00 hours G.M.T. except for an anemometer at 40 ft. which gave a continuous record. These data are not tabulated here, but may be seen in the records kept by this Department.

Identification of Aphids.

Wherever possible identification has been made down to species ; but there are some genera for which this is impossible owing to lack of adequate keys. Sometimes identification even to the genus was impracticable and, in the absence of keys to the alatae, would have entailed a disproportionate expenditure of time in identifying from collections ; all aphids in this category have been listed as " unidentified." The remaining class referred to as " unidentifiable " contains those insects so damaged as the result of treatment subsequent to capture that it was impossible to place them within a genus.

3. Species of Aphids Caught.

Trapping in 1947 started on 23rd June and ended on 13th November. The total catch of aphids was 4744. The data are displayed in Tables Ia, b and c.

When the daily catches of aphids are considered (fig. 1) the most evident feature is the occurrence of two well-marked peaks, and an intervening period during August when the catch is at a minimum. The first of these peaks which occurs mainly in July is principally due to the redistribution of alatae flying between secondary hosts; the second peak extending over September and October at the time of flights from secondary back to primary hosts. Unfortunately trapping was started too late to include the peak due to spring migration from primary to secondary hosts. An example of this, together with the July peak, is shown by Doncaster and Gregory (1948).

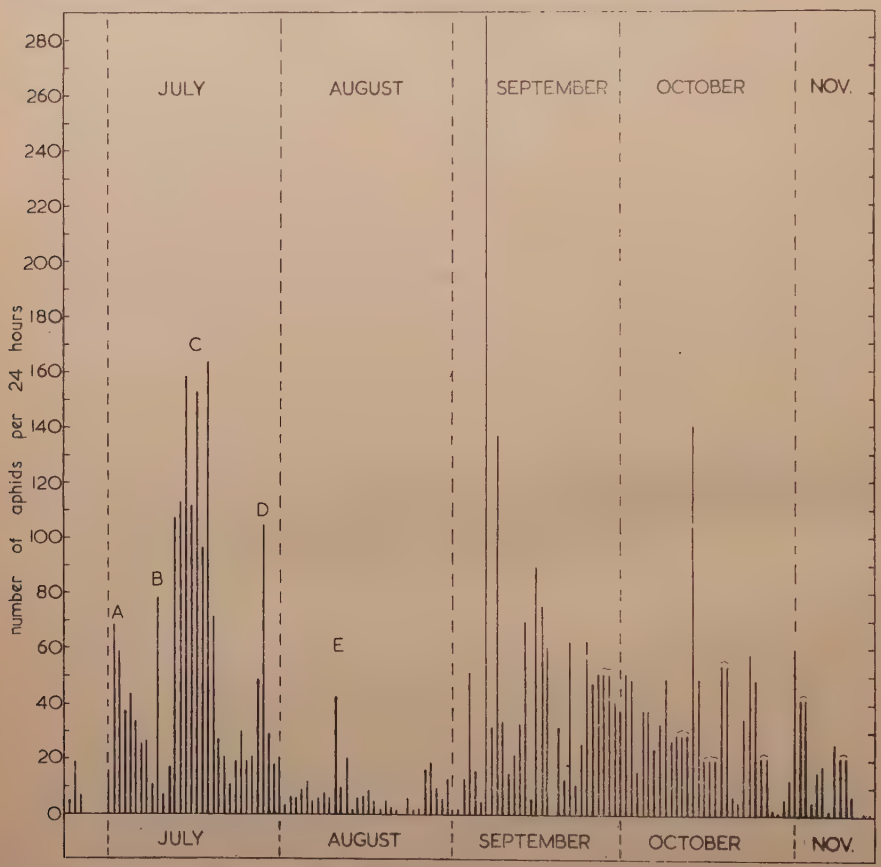

FIG. 1.—Total aphids, male and female, caught in successive 24-hourly periods in suction trap at Rothamsted, 1947. Bracketted days indicate a 2-day catch divided between the two days.

(*a*) *Species Constituting the Two Principal Peaks of Abundance.*

The July peak.—Most of the common species found in the July peak also occurred during September to October; the exceptions were *Metopolophium dirhodum* (Walker) and *Rhopalosiphum nymphaeae* (Linn.), neither of which appeared from August to November; the relative proportions of some of these species are, however, very different in the two peaks. The July peak

showed a very high proportion of grass feeders, *M. dirhodum* being the commonest species. The comparatively high proportion of *R. insertum* may possibly be attributed to a small orchard 100 yds. from the trap. All the aphids in the July peak were females except for one *B. helichrysi* and two unidentified males.

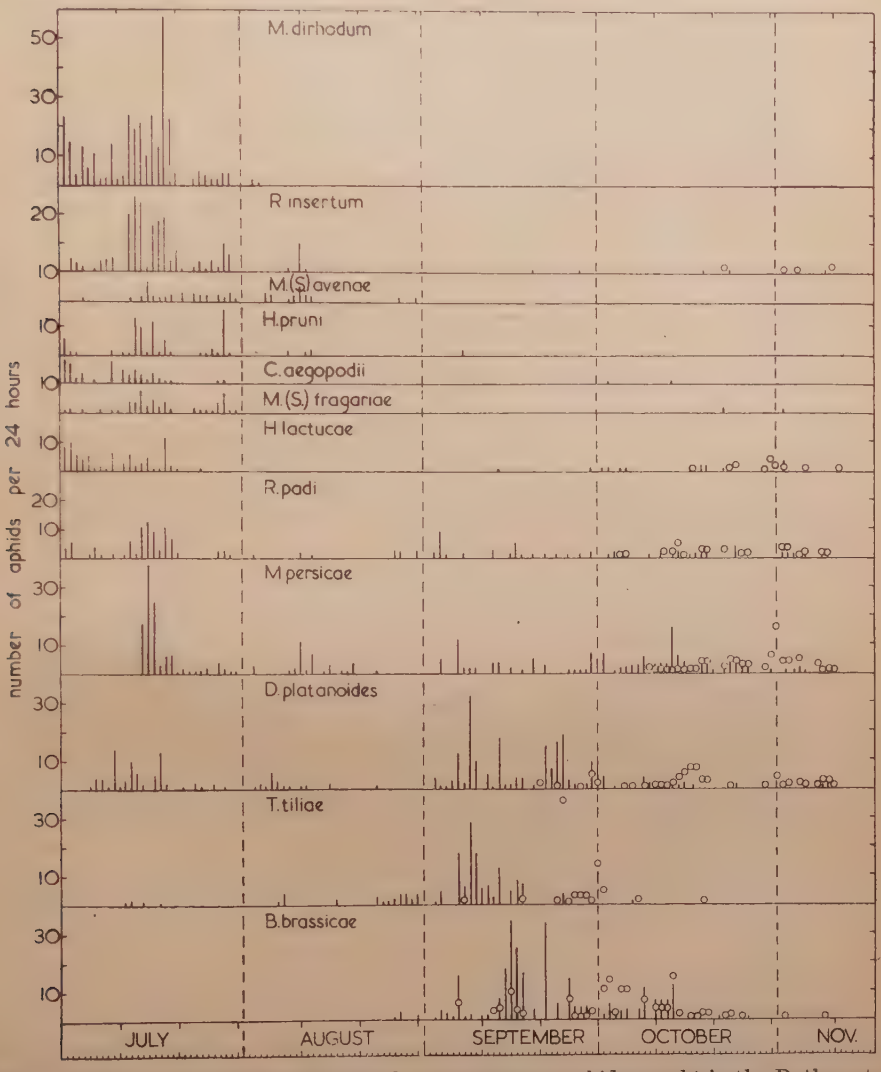

FIG. 2.—The succession of abundance of the commonest aphids caught in the Rothamsted suction trap, 1947. 0 = males ; 1 = females.

The September-October peak.—The commonest species were *B. brassicae*, *M. persicae*, *A. corni*, *Therioaphis tiliae* and *D. platanoides*. The occurrence of winged males in the trap was confined, with 4 exceptions, to the September-October peak. The order of commonness of the males is somewhat similar

to that of the females. But although the order was similar the proportion of males to females of various species was different ; this proportion should not, however, be regarded as a normal sex ratio, since the females concerned were all parthenogenetic migrantes from which the sexual females would eventually develop.

B. brassicae, *Cryptomyzus ribis* (Linn.), *Eriosoma lanigerum* (Hausm.) and *Aploneura lentisci* (Pass.) were species which did not occur during June-August.

(*b*) *Succession of Species.*

The subsidiary peaks within the July and the September-October ranges are due to a differential fluctuation in density of a number of species.

The July peak (fig. 1) is composed of four subsidiary peaks, A, B, C and D, followed by a small peak, E, in August. Fig. 2 shows how these peaks are composed of the varying abundance of the commoner aphid species. For example, the decline after peak A is due to a general decline of aphids caught but particularly of *M. dirhodum*, *H. lactucae*, *C. aegopodii*, *H. pruni* and *R. insertum*. Peak B is due to a high catch of *M. dirhodum*, *C. aegopodii*, *H. lactucae* and *D. platanoides*. Peak C is composed of all the species present in A but reinforced by a sudden influx of *M. persicae*.

The separate fluctuations within peak C are similarly differentially constituted. Peak D is composed almost entirely of *H. pruni*, *M. fragariae*, and *R. insertum*, while *M. avenae*, *R. insertum* and *M. persicae* are responsible for the August peak (E).

The September-October peak is much more complex, since not only are more species involved but males are present as well. Attention is drawn to an exceptional day, the 6th of September, when 281 aphids were caught in the 24 hours and are represented as a peak which rises suddenly from the generally low level (fig. 1). The insects of this peak were nearly all *Aphis* species—probably mostly of one species, but it was not in our power to identify beyond the genus. It was a sudden flighting of a species not generally among the commonest found in the trap.

4. Additions to Kloet and Hincks "A Check List of British Insects."

The following species which have occurred in the traps in 1947 are not listed in Kloet and Hincks (1945) Further details of these insects are to be published by H. L. G. Stroyan.

Eulachnus blunki Börner.
Periphyllus granulatus (Koch).
**Cavariella archangelicae* (Scop.).
Cavahyalopterus mühlei Börner.
**Metopolophium albidum* Lambers.
**Metopolophium tenerum* Lambers.
Acrythosiphum caraganae (Cholod.).
Macrosiphoniella chamomillae Lambers.

Species marked with an asterisk have already been recorded from Britain by Broadbent and Doncaster (1949).

Summary.

1. From June to November, 1947, a suction trap was operated 5 ft. above ground level at Rothamsted. The numbers and species of aphids caught each day may be considered as approximately equivalent to their densities in the air.

2. During the trapping period two seasonal peaks of capture are shown: one over July, one over September-October. Within these peaks daily fluctuations occur. The aphid species and their relative numbers are compared within and between each peak and the daily succession of common species analysed quantitatively.

3. Five species new to Britain are recorded.

Acknowledgments.

It is a pleasure to acknowledge the help given by Drs. L. Broadbent, I. Thomas and H. R. Lambers with identification.

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[*See pages 22-24 for Table I A-C*

TABLE Ia. - *Aphids Caught in Rothamsted Suction Trap from 23rd June to 19th August*, 1947.*

	June.		July.						August.				Total.
	23–25.	26–30.	1–5.	6–10.	11–15.	16–20.	21–25.	26–31.	1–5.	6–10.	11–15.	16–19.	
Protrama radicum (B. de F.)	.	.	.	.	.	.	.	.	.	1	1	.	2
Anoecia corni (Fabr.)	.	.	4	.	8	6	1	4	2	.	.	1	26
Eulachnus spp.	.	.	.	1	1	1	.	.	.	.	.	.	3
Vacuna dryophila (Schr.)	.	.	.	.	1	1	1	.	.	.	.	.	3
Sipha glyceriae (Kalt.)	.	.	.	.	.	.	2	.	.	.	.	.	2
Caricosipha paniculata Börner	.	.	.	.	1	.	.	.	.	.	.	.	1
Myzocallis annalata (Hartig)	1	.	.	.	1	2	3	.	.	.	.	.	7
,, *castanicola* Baker	.	.	.	.	1	.	.	.	.	.	.	.	1
,, *coryli* (Goetze)	.	.	.	.	.	1	.	.	.	.	.	.	1
,, spp. unident.	.	.	1	.	.	.	1	3	1	1	.	1	8
Therioaphis tiliae (Linn.)	.	.	.	.	4	1	.	.	.	5	.	2	12
Euceraphis nigritarsus (Heyden)	.	.	.	.	2	.	.	.	.	.	.	.	2
Drepanosiphum platanoides (Schr.)	1	.	1	24	21	20	4	3	10	6	3	.	93
Aphis spp.	6	1	26	11	72	96	37	85	6	9	14	4	367
Brachycaudus rumexicolens (Patch)	.	.	.	.	6	3	.	.	.	.	.	.	9
,, spp. unident.	.	.	1	1	2	2	.	1	.	.	.	.	7
,, *helichrysi* (Kalt.) ♂	.	.	.	.	1	.	.	.	.	.	.	.	1
Sappaphis spp.	.	.	1	.	.	3	.	.	.	.	.	.	4
Anuraphis subterranea (Walk.)	1	.	.	.	.	.	.	.	.	.	.	.	1
Rhopalosiphum insertum (Walk.)	2	.	10	14	72	64	8	23	.	12	1	.	206
,, *nymphaeae* (Linn.)	.	.	.	.	.	.	4	1	.	1	.	.	6
,, *padi* (Linn.)	1	1	11	7	32	32	.	7	1	2	1	.	95
Hyadaphis sp.	.	.	.	.	1	.	.	.	.	.	.	.	1
Cavariella aegopodii (Scop.)	2	2	21	9	17	8	.	2	.	.	.	.	61
,, *pastinaceae* (Linn.)	.	.	.	.	.	1	.	.	.	.	.	.	1
,, *theobaldi* Gill. and Bragg	1	.	1	.	1	.	.	.	.	.	.	.	3
Hyalopterus pruni (Geoffr.)	.	.	8	2	26	19	2	21	.	1	3	.	82
Hayhurstia atriplicis (Linn.)	.	.	1	1	10	13	.	.	.	.	.	.	25
Cavahyalopterus mühlei Börner	.	.	.	.	1	.	.	.	.	.	.	.	1
Brachycolus sp.	.	.	.	.	.	.	.	1	.	.	.	.	1
Capitophorus hippophaes (Walk.)	.	.	.	.	2	.	.	.	.	.	.	.	2
,, *flaveolus* (Walk.)	.	.	1	.	.	.	.	.	.	.	.	.	1
,, spp. unident.	.	.	.	.	3	7	2	3	.	1	2	1	19
Cryptomyzus galeopsidis (Kalt.)	.	.	.	.	1	4	.	.	.	.	.	.	5
Pentatrichopus fragariae (Theob.)	.	.	.	.	.	.	.	1	.	.	.	.	1
Phorodon humuli (Schr.)	.	.	1	2	2	.	.	.	.	.	.	.	5
Ovatus crataegarium (Walk.)	.	.	.	2	.	.	.	.	.	.	.	.	2
,, *menthae* (Buckt.)	.	.	3	.	3	1	.	.	.	.	.	.	7
,, sp. unident.	.	.	.	.	.	.	.	1	.	.	.	.	1
Hyperomyzus lactucae (Linn.)	4	4	34	10	19	17	1	.	.	.	.	.	89
Megoura viciae (Buckt.)	.	.	1	.	.	1	.	1	.	.	.	.	3
Nasonovia ribis-nigri (Mosley)	.	1	2	2	4	3	1	1	.	1	1	.	16
Myzus cerasi (Fabr.)	.	.	.	.	1	.	.	.	.	.	.	.	1
,, *persicae* (Sulz.)	.	.	.	.	55	42	7	13	3	14	12	6	152
,, spp.	.	.	2	.	.	.	.	5	1	.	.	1	9
Metopolophium albidum Lambers	.	.	.	.	1	.	.	.	.	.	.	.	1
,, *dirhodum* (Walk.)	2	5	60	33	77	121	10	12	3	.	.	.	323
,, *tenerum* Lambers	.	.	.	.	1	.	.	.	.	.	.	.	1
Acyrthosiphum caraganae (Cholodk.)	.	.	.	.	1	.	.	.	.	.	.	.	1
,, *pisum* (Harris)	.	.	3	2	7	5	.	3	2	2	1	.	25
Macrosiphum cholodkovskyi (Mordw.)	.	.	.	.	.	.	.	.	.	.	1	.	1
,, *euphorbiae* (Thos.)	.	.	.	.	.	1	.	.	.	2	.	.	3
,, sp. unident.	.	.	.	.	.	.	.	.	.	.	.	1	1
,, (*Sitobion*) *avenae* (Fabr.)	.	.	1	.	10	7	10	10	5	9	4	.	56
,, ,, *fragariae* (Walk.)	.	1	4	3	19	13	4	14	.	.	.	.	58
,, ,, sp. unident.	.	.	.	.	.	.	1	.	.	.	.	.	1
Dactynotus achilleae (Koch)	.	.	4	2	11	9	1	1	.	.	.	.	28
,, *cirsii* (Linn.)	.	.	.	.	.	.	.	.	.	.	1	.	1
,, *hypochoeridis* Lambers	.	.	.	.	.	1	.	.	.	.	.	.	1
,, spp. unident.	.	.	.	.	1	1	.	3	.	.	.	.	5
,, (*Uromelan*) *jaceae* (Linn.) grp.	.	.	2	.	.	4	.	2	1	.	.	.	9
Macrosiphoniella chamomillae Lambers	.	.	.	.	.	.	.	.	.	.	1	.	1
,, spp. unident.	.	.	.	.	1	.	.	1	.	.	.	.	2
Eriosoma ulmi (Linn.)	1	.	1	.	1	.	.	.	.	.	.	.	3
,, spp. unident.	2	.	.	.	.	.	.	.	.	.	.	.	2
Tetraneura ulmifoliae Baker	1	.	3	.	.	.	.	.	.	.	.	.	4
Pemphigus bursarius (Linn.)	.	.	1	.	.	.	.	.	.	.	.	.	1
Thecabius affinis (Kalt.)	1	.	.	.	4	.	.	.	.	.	.	.	5
Unidentified	5	.	3	3	3	4	.	16	3	.	.	4	41
,, males	.	.	.	.	.	.	.	2	.	.	.	.	2
Unidentifiable aphids	.	1	32	21	2	.	.	3	.	1	.	.	60
Total	31	16	244	150	510	514	100	243	38	68	46	21	1981

* All females except 3.

TABLE IB.- *Female Aphids Caught in Rothamsted Suction Trap Between 20th August and 13th November, 1947.*

	August.			September.						October.						November.			Total.
	20–25.	21–31.	26–31.	1–5.	6–10.	11–15.	16–20.	21–25.	26–30.	1–5.	6–9.	10–15.	16–20.	21–26.	27–31.	1–5.	6–10.	11–13.	
Protrama radicum (B. de F.)			2	1					1										4
Anoecia corni (Fabr.)			5	6	17	11	21	16	28	21	34	35	16	17	5	22	9		263
Eulachus blunki Börner				1	9		2							1					13
,, spp.				1						1									2
Pterocomma salicis (Linn.)										1									1
Periphyllus granulatus (Koch)							1												1
,, *testudinatus* (Thornton)												1							1
Chaitophorus sp.				1															1
Myzocallis annulata (Hartig)					1	1	3					1							6
,, *castanicola* Baker					3	4	2	2	4	4	1	1		1					22
,, *coryli* (Goetze)				1		1													2
,, spp. unident.				1	2														3
Therioaphis tilae (Linn.)		5	16	6	78	28	16	4			1								154
Calaphis betulicola (Kalt.)					1	1													2
Chromaphis juglandicola (Kalt.)					1														1
Euceraphis nigritarsus (Heyden)									3			5		1					9
Drepanosiphum acerina (Walker)			1																1
,, *platanoides* (Schr.)		1		9	58	28	11	60	27	5	7	10	1	2	2	2	2		225
Aphis spp.	2	1	9	11	233	20	31	7	8	18	3	21	6	1	1	2	1		375
Brachycaudus cardui (Linn.)							1	1		3									5
,, *helichrysi* (Kalt.)					1	1													2
,, *rumexicolens* (Patch)						3	2			1									6
,, spp. unident.						1	1					1		2					5
Sappaphis spp.					1		8	1	1	7	2	4		1		1			26
Ceruraphis eriophori (Walker)						1						1							2
Anuraphis subterranea (Walker)				1	1														2
Rhopalosiphum insertum (Walker)							1		1				1	1			1		5
,, *padi* (Linn.)			7	12	1	5	7	3	3	4	1	4	7	7		7	2		70
Schizaphis spp.				3	1	1													5
Hyadaphis spp.			1				3			1									5
Cavariella aegopodii (Scop.)										1		1							2
,, *archangelicae* (Scop.)								1											1
,, *theobaldi* Gill. and Bragg.						1				1									2
Brevicoryne brassicae (Linn.)			6	9	19	63	46	55	17	16	15	34	1	4		2			287
Hyalopterus pruni (Geoffr.)					2														2
Hayhurstia atriplicis (Linn.)			1																1
Aspidaphis polygoni (Walk.)				1															1
Capitophorus hippophaes (Walk.)					12	2	1	2	2	2	2	1				1			25
,, *flaveolus* (Walk.)			1		1			1			2	2						1	8
,, spp. unident.			1	3						1	1								6
Cryptomyzus ribis (Linn.)					1														1
Phorodon humuli (Schr.)										1									1
Ovatus menthae (Buckt.)							1												1
Hyperomyzus lactucae (Linn.)						1			1	4			4	3		3			16
Nasonovia ribis-nigri (Mosley)											1		1						2
Myzus cerasi (Fabr.)			1					1		3	2		3						10
,, *ornatus* Laing											1								1
,, *persicae* (Sulz.)		1		5	18	10	6	4	16	12	14	35	15	19	5	5	1		166
,, spp.		1								1									2
Acyrthosiphum pisum (Harris)		1				2													3
Macrosiphum euphorbiae (Thos.)				1			2							2					5
,, *funestum* (Macch.)						1													1
,, *rosae* (Linn.)								1	1			1							3
,, sp. unident.				1															1
M. (Sitobion) avenae (Fabr.)			2											2		1			2
,, ,, *fragariae* (Walk.)																			3
Dactynotus sonchi (Geoffr.)								1											1
Macrosiphoniella sanborni (Gill.)												1							1
Eriosoma lanigerum (Hausm.)					2		1			1						1			5
,, *ulmi* (Linn.)																2			2
Tetraneura ulmifoliae Baker					1							1							2
Geoica spp.					2														2
Pemphigus bursarius (Linn.)			1	1	2	2	1			3	1	5	9	15		1	4		45
Thecabius affinis (Kalt.)							2	1	3	4	1	6	2	1			1		21
Aploneura lentisci (Pass.)			1		1														2
Unidentified		2	10	5	5	5		1		3									31
Unidentifiable				5	21	1			73		28	1	1	42	31	2	22		227
Total	2	12	65	85	495	194	170	162	189	119	117	172	67	122	44	52	43	1	2111

TABLE IC. *-Male Aphids Caught in Rothamsted Suction Trap Between 20th August and 13th November*, 1947.

	August.		September.						October.						November.			Total.
	20–25.	26–31.	1–5.	6–10.	11–15.	16–20.	21–25.	26–30.	1–5.	6–9.	10–15.	16–20.	21–26.	27–31.	1–5.	6–10.	11–13.	
Cinara sp.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.		1
Eulachnus spp.	.	.	.	.	1	.	1	1	.	.	.	5	.	.	.	.		8
Periphyllus spp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1		3
Chaitophorus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1		1
Myzocallis spp.	.	.	.	.	.	.	1	.	4	.	8	12	1	.	3	1		30
Therioaphis tilae (Linn.)	.	.	.	1	.	2	38	23	5	1	.	1	.	.	.	.		71
Euceraphis nigritarsus (Heyd.)	.	.	.	.	.	.	.	.	.	.	2	.	1	1	4	2		10
Drepanosiphum platanoides (Schr.)	.	.	.	.	.	2	1	8	1	2	15	21	1	5	6	8		70
Phyllaphis fagi (Linn.)	.	.	.	.	.	.	.	.	.	.	1	3	.	1	.	1		6
Aphis spp.	.	.	.	.	8	3	1	2	9	4	30	9	11	.	7	1		85
Brachycaudus rumexicolens (Patch)	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.		1
,, spp.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	.		4
Sappaphis spp.	.	.	.	.	.	.	.	.	1	.	11	1	4	.	6	1		24
Rhopalosiphum insertum (Walk.)	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	2		6
,, *padi* (Linn.)	.	.	.	.	.	.	.	.	2	.	10	5	7	.	10	3		37
Brevicoryne brassicae (Linn.)	.	.	.	7	17	5	7	8	48	7	31	6	4	.	1	1		142
Capitophorus hippophaes (Walk.)	.	.	.	.	.	.	.	.	1	.	2	1	1	.	1	.		6
,, *flaveolus* (Walk.)	.	.	.	.	.	.	.	.	.	.	1	1	5	.	3	1		11
Cryptomyzus ribis (Linn.)	.	.	.	.	.	.	.	.	1	.	.	3	1	.	3	.		8
Hyperomyzus lactucae (Linn.)	.	.	.	.	.	.	.	.	.	.	.	1	3	7	.	2	1	14
Megoura vicae (Buckt.)	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.		1
Nasonovia ribis-nigri (Mosley)	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.		2
Myzus cerasi (Fabr.)	.	.	.	.	.	.	.	.	.	.	.	2	2	.	3	4		11
,, *persicae* (Sulzer)	.	.	.	.	.	.	.	.	.	2	7	11	17	24	13	6		80
,, spp.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.		3
Unidentified	.	2	2	2	.	.	.	.	.	.	5	.	2	.	1	1		15
Unidentifiable	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.		2
Total	0	2	2	12	27	12	49	42	72	16	124	86	65	38	70	34	1	652

BLOOD-CELL COUNTS IN THE AFRICAN MIGRATORY LOCUST (*LOCUSTA MIGRATORIA MIGRATORIOIDES* REICHE & FAIRMAIRE).

By D. P. WEBLEY, B.Sc., D.I.C., F.R.E.S.
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INTRODUCTION.

Examination of the literature reveals that little critical research has been carried out on the haemocytes of Orthoptera. This present work deals with some aspects of the physiology of the blood cells, and does not touch their morphology. The original aim was to compare the effects of some insecticides upon the number of cells in unit volume of the blood (blood-cell count), but since the normal blood picture of *Locusta* had not been worked out, and time was limited, it was decided to devote the whole time to the study of the normal blood picture.

The blood-cell counts in published work are few. Only three papers present a series of results which are of any great value. Tauber & Yeager (1934) worked on the blood-cell count of the American Field Cricket (*Gryllus assimilis pennsylvanicus* Burm.). Their paper presents an analysis of 220 blood counts. It was found that the entire series had a tri-modal frequency distribution, that this characteristic distribution was not due to maleness or femaleness, to the difference between nymph and imago, to the anti-coagulant action of glacial acetic acid, to the month when collected, or to the existence of two broods that overwinter, respectively, in the egg and nymphal stages. They suggested that the distribution might be at least partly explained by the occurrence of excessively high total blood-cell counts accompanying certain physiological and pathological conditions, such as ecdysis, oviposition, and parasitization. The total blood-cell count ranged from 15,000 to 275,000, with an average of 70,000 cells per cubic mm. It was found that the average count for the imago was higher than that for the nymph. Unfortunately the insects were collected at random in the field at different times of the year, and therefore the environmental conditions were not controlled. There was no check upon the age or weight of the animals, their nymphal stage, or other critical points in their life history, e.g. whether the females were about to or had oviposited. The paper is of great value, however, because the results were thoroughly analysed.

H. W. Smith (1938) gives a series of results for *Periplaneta americana* (L.). He found an average count of about 89,000 cells per c.mm. The cockroaches were kept at a constant temperature and humidity, but no information was given as to their age or their instar.

The only paper dealing with blood-cell counts in locusts is that of Mathur & Soni (1937), who worked on *Schistocerca gregaria* (Forsk.). These insects were bred under laboratory conditions, but the number of insects operated on was too small for the counts to be statistically valuable. The counts given were as follows:

1st Stage hoppers	220 cells per c.mm.
2nd ,, ,, ...	390 ,, ,,
3rd ,, ,, ...	1,180 ,, ,,
4th ,, ,, ...	3,000 ,, ,,
5th ,, ,, ...	5,000 ,, ,,
Young adults, sex not stated .	6,000/6,500 ,, ,,

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These authors were able to correlate the rise in blood-cell count with the diminution with age of the amount of fat globules in the haemolymph.

All these workers used a similar technique, the basis of which is the work of Fischer (1934)—a modification of the haemocytometer technique used in human physiology. The main modification was to treat the animal before sampling with a blood anti-coagulant, namely, glacial acetic acid.

Material.

The insects, *Locusta migratoria migratorioides* R. & F. (*transiens*, approaching *gregaria* phase), were obtained from the Anti-Locust Research Centre, London. In order to get an adequate supply of known age, the locusts were reared from first and second stage nymphs in a large glass tank with a 3–4 in. layer of sand on its floor. The tank was heated by electric bulbs, arranged to give temperatures between 25° and 30° C.; the insects were thus given a choice of temperature. On emergence as adults they were marked with coloured paints on the thorax according to the date (each separate day having its known colour and position on the thorax), and transferred to one of two large square asbestos-lined cages kept at a similar temperature. They were kept there until used for experiment. They were supplied with fresh grass twice or three times a day, the grass being mostly young leaves of *Holcus lanatus* and *Dactylis glomerata*. This food, with such frequent changes, gave a fairly constant relative humidity to the cages.

The Migratory Locust was chosen for this work because of its large size and the ease with which it may be bred. The size of the insect is obviously of great importance in any study of haemolymph, since one wishes to obtain as much blood as possible for the haemocytometer pipette, without any squeezing of the insect. Although *Locusta* is a large insect, there is still difficulty in extracting blood from it in some cases, old males (30 + days) being extremely short of haemolymph and "dry." This is in direct contrast to newly emerged young adults, which yield a copious supply of blood.

Apparatus and Technique.

The haemocytometer used was one of the double chamber type with improved Neubauer Ruling. A British Standard Specification white cell pipette, normally used for human physiological work, was used for all counts, the dilution depending upon the amount of blood easily obtained. Tauber & Yeager (1934) and Smith (1938) used a modified blood pipette. My pipette could carry a maximum of 1 c.mm. of blood, which could be diluted to 1 in 10.

The diluting fluid was as used by Tauber & Yeager. It consisted of ·081 M NaCl; ·002 M KCl; ·001 M $CaCl_2$; ·005 per cent. gentian violet, and 0·125 per cent. glacial acetic acid.

The technique began with the treatment of the insect with a blood anti-coagulant. Previous workers used two methods:

(*a*) The killing of the insect in water heated to 55° C.

(*b*) The suspending of the insect in glacial acetic acid vapour.

Both methods were based upon fixing the blood cells by precipitating proteins. In the present work the glacial acetic acid method was used. It consisted of suspending the insect in the acid vapour for 10–15 minutes.

Each insect, after remaining in the vapour for the required length of time,

was removed and weighed. The blood was then obtained by holding the abdomen across one's first finger (the head being held under the thumb, while the apex of the abdomen was bent between the first and second fingers) and snipping off one of the large hind legs at the coxa. The blood was immediately drawn into the pipette to the required dilution, together with sufficient diluting fluid, until the total volume was brought up to the 11 mark. The slight bending of the abdomen caused sufficient pressure to allow a free escape of blood. The pipette was then shaken vigorously for one to two minutes, after which the first few drops of diluted blood in the pipette stem were rejected and the remainder introduced down the grooves of a clean, complete haemocytometer slide into the counting chambers. The slide was then set in the mechanical stage of the microscope and left for a minute to allow any fluid movement in the chambers to stop.

Other workers have used the antennae (Smith, 1938) and the cervix (Mathur & Soni, 1937) as the source from which blood was removed, but these places did not produce a satisfactory supply in *Locusta*, the best supply being obtained from the cut hind coxa.

After all movement had stopped the blood cells were counted. All touching the base of each square and the left-hand vertical side were included in that square, while any touching the other two sides were ignored. Altogether 320 blood counts were made in this manner.

Results.

(a) *Nymphs.*

2nd stage nymphs.—Owing to the difficulty of obtaining a sufficient quantity of blood from nymphs in this instar, because of their small size, only two results were obtained; these gave an average of 6,834 cells/mm.^{3}

3rd, 4th, 5th stage nymphs.—In order to estimate the age of an insect within its instar (since it was found impracticable to mark nymphs with coloured paints) all nymphs were weighed and all relevant information, such as hardness or softness of cuticle, was noted. The weights were then divided into three groups according to size, the lightest animals being considered the youngest and the heaviest the oldest of that instar. Each figure in Table I is the average of 5–10 experiments.

Table I.—*Blood-Cell Count and Weight of Nymphal Stages.*

		Males.			Females.	
		Wt. (gm.).	Cells/mm.^{3}		Wt. (gm.).	Cells/mm.^{3}
3rd	N	·074– ·097	6,336	N	·083– ·144	7,029
	M	·098– ·122	13,352	M	·145– ·206	10,420
	O	·123– ·148	11,091	O	·207– ·269	10,296
4th	N	·118– ·219	6,861	N	·125– ·287	7,112
	M	·220– ·321	6,992	M	·288– ·450	7,670
	O	·322– ·426	7,768	O	·451– ·616	9,359
5th	N	·331– ·583	5,675	N	·362– ·650	7,597
	M	·584– ·836	8,208	M	·651– ·939	5,491
	O	·837–1·09	8,729	O	·940–1·23	7,202

N = Newly emerged; M = middle of instar; O = end of instar.

Difference between sexes.—The average count for males was 7,073, while that for females was 6,797. The difference is not significant.

Changes within each instar.—In both sexes and in practically all the instars there is one common fact: the concentration of cells was lower at the start and higher at the end of any instar, and there was a sharp drop at moulting.

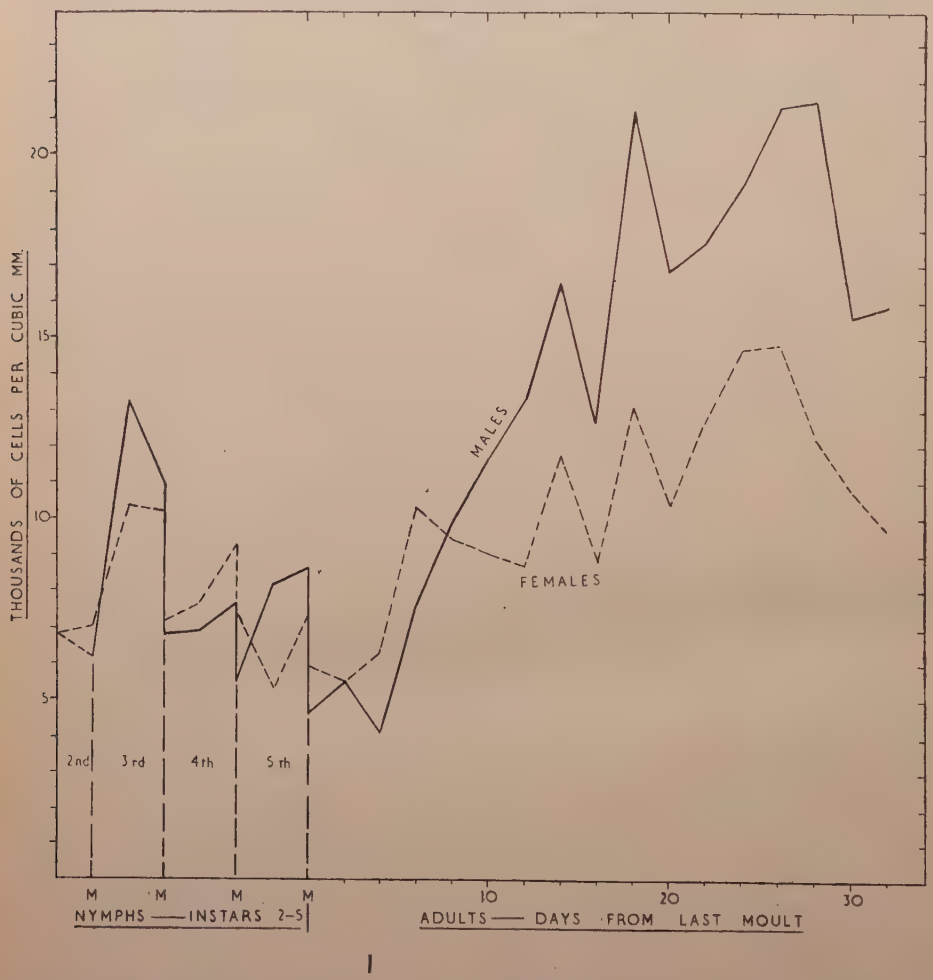

Fig. 1.—The changes in blood-cell counts with advancing age in *Locusta*. For the adults a time-scale of days is used, but for the nymphs the instar lengths are shown as if equal, for convenience of scale, with the moults indicated (M). There is a sharp fall in blood count at each moult and a rise during early adult life.

The only exception comes from 5th instar females, where newly moulted animals had a rather high concentration of cells, higher than at any later time in that instar. For the central part of an instar the counts were sometimes low, like the earlier ones, and sometimes high, like the later ones (Table I and fig. 1), and the data are inadequate for showing the course of the changes.

The third instar was peculiar in showing a very large increase in all counts. This may be associated with the profound metabolic changes taking place at that time, including the great growth and turning of the wing rudiments (Roonwal, 1940).

Distribution of results.—When the results are arranged in the form of a histogram (fig. 2) in which the counts are arranged in class intervals of 1,000 cells/mm.^{3}, for females there are peaks at 3, 7 and 11 thousand cells/mm.^{3}, while for males there is a more uniform distribution with higher frequencies at 3, 5, 6, 8 and 11 thousands.

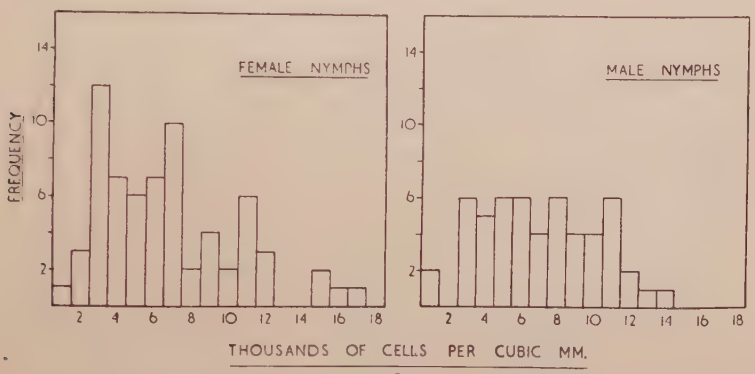

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FIG. 2.—Frequency distributions of the blood-cell counts for female and male nymphs separately. The high counts come predominantly from the 3rd instar.

When the figures for the 3rd instar are left out there is less sign of the peak at 11,000. The occurrence of the three peaks may be explained, at least partially, by the following factors:

(*a*) Low counts at time of emergence.
(*b*) High counts at end of instar.
(*c*) A phenomenal increase in cell numbers in the 3rd instar.

(b) *Influence of Ecdysis.*

The most striking feature of the blood counts of hoppers was the immediate and large fall which always occurred at a moult (fig. 1). There are two possible explanations of this:

(1) There might be a real drop in the number of cells in the haemolymph, due, for example, to their becoming attached to tissue surfaces.
(2) Without any change in the number of cells, since the cell counts represent concentrations there might be a change in the volume of haemolymph.

Now there are two recognizably different kinds of haemocytes in the blood —fusiform and non-fusiform. If the drop in cell count were simply due to dilution or concentration, the fusiform/non-fusiform ratio (Yeager, 1945) would not change; but if it were due to attachment, and if the two kinds were diffe-

rently affected, the ratio would change. For convenience the last ecdysis was chosen, so that the late 5th instar and newly emerged adults were compared. The cells were counted by making uniform blood smears, staining with Giemsa's blood stain, and classifying the cells under ten microscope fields into fusiform and non-fusiform. Two smears were taken from each specimen, and two specimens were used for each age.

In the late 5th instar 70 per cent. of the cells were fusiform, while the newly emerged adult had 69 per cent. There is no significant difference in the ratio, and therefore either the two types of cell are withdrawn from the blood in the same proportion, or the change in concentration of cells has been brought about

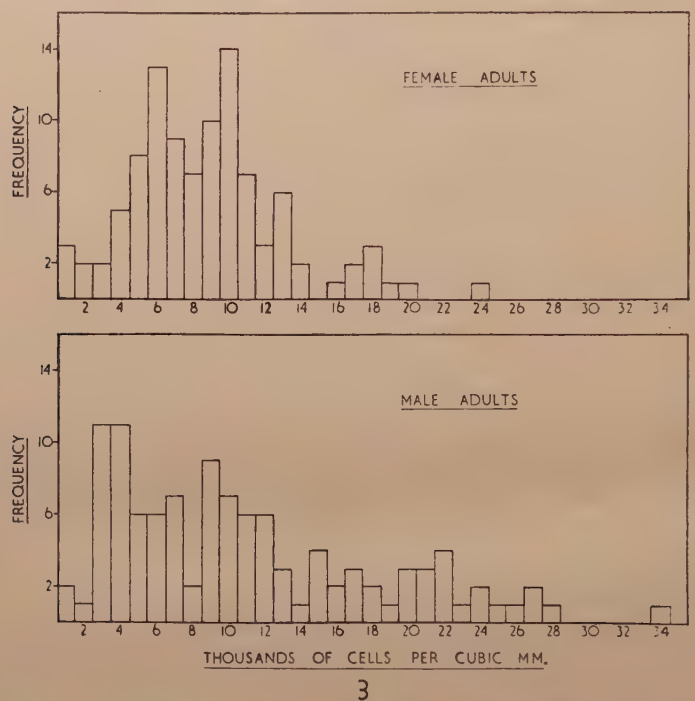

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Fig. 3.—Frequency distributions of the blood-cell counts for female and male adults separately. The high counts come predominantly from older animals.

by the acquisition of water by the lymph. The former suggestion does not appear to be likely, since one would expect more phagocytic cells to be released at this time. The latter suggestion seems much more likely ; Mellanby (1939) has stated that blood has water-storing powers.

(c) *Adults.*

Males and females.—The average count for all adults was 9,024 cells/mm.^{3} Comparison of the male and female averages shows that the male average count, 11,495, was significantly greater than that of the female, 8,810 (fig. 3), and the excess was fairly consistent from one week after emergence onwards (fig. 1).

(d) *Adult Males.*

In male adults the average count was 11,495 cells/mm.^{3} From fig. 3 it can be seen that a number of peaks are present, especially at (1) 3–4,000 cells, (2) 9000 cells, (3) 22,000 cells/mm.^{3}

The effect of age on count.—Table II and figs. 1 and 4 show how counts vary with age. Each figure is the average from 5–10 experiments.

For the first four days after the final moult the count was constant at an average value of 4,600, after which it rose consistently until on the 14th day it reached about 16,600 cells/mm.^{3} The weight of the insect rose in a similar way up to about the 14th day—the time when it is mature and able to fertilize the female. Thus for the 3rd–14th days, the correlation of cell count and age was 0·949 ($p < 0·001$), and of weight and age was 0·958 ($p < 0·001$) (10 points). After that both weight and cell-count fluctuated, but weight no longer rose, while cell-count did. Fig. 5 shows that there is a good correlation between weight and count up to this time, but afterwards there is constancy in weight but increase in cell count.

TABLE II.—*Blood-Cell Counts and Weights of Adult Males in Relation to Age.*

Days old.	Av. count.	Av. weight. (gm.).
Newly emerged	4,682	0·77
1–2	5,437	0·908
3–4	4,075	1·126
5–6	7,512	1·214
7–8	9,867	1·375
9–10	11,608	1·47
11–12	13,350	1·579
13–14	16,593	1·54
15–16	12,719	1·53
17–18	21,256	1·59
19–20	16,851	1·37
21–22	17,675	1·59
23–24	19,241	1·55
25–26	21,378	1·31
27–28	21,400	1·65
29–30	15,560	1·67
31–33	15,805	1·39
60–70	22,312	1·41

Moisture.—It was thought that the increase in blood-cell count during the 3rd–14th days might be correlated with a loss of water, the blood cells becoming increasingly concentrated by the reduction of the water content of the blood plasma. Mellanby (1939) has suggested that one of the functions of insect blood is to act as a reservoir of water. The moisture content of young adult locusts was obtained (fig. 4) by heating them at 101°–103° C. until their weights were constant. The moisture content is expressed in terms of percentage of wet weight. Examination of the graph (fig. 4) indicates that there was a drop in the percentage of water from 77 per cent. to 65 per cent. in the first ten days of life.

The real meaning of this relation between cell counts and percentage water content is not clear. The drop in percentage water content in the first ten days was accompanied by a considerable rise in total weight; this rise can be seen to be mostly due to an increase of dry material to over twice the initial adult value, but the total amount of water rises too, by nearly 40 per cent. If there were no other changes, an increase in dry weight by the addition of fat would not involve much increase in water, so that the percentage dry weight

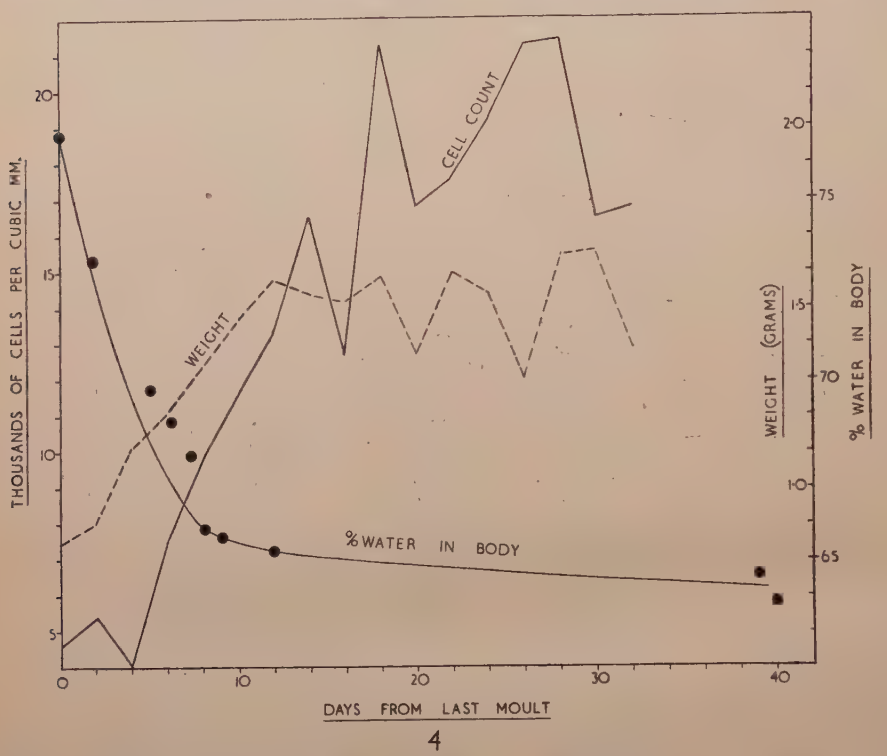

Fig. 4.—Changes in cell count, weight and water content of body of adult males. The weight and water content become approximately stable after about 10 days, but the cell count continues to rise for a further week.

would rise. The figures given above do not, therefore, indicate what happens to the volume of blood. But it is noteworthy that the cell count continues to rise steeply for about a week after the weight and the moisture content have become fairly steady, so that there is either a real rise in the number of blood cells or a fall in blood volume after the gross measures of weight and water content have stabilized. It is certainly more difficult to extract a good quantity of blood from older locusts than from younger ones.

(e) *Adult Females.*

The average count for female adults was 8,810. In fig. 3 the histogram again has several peaks, at 6, 10 and 18 thousand cells per c.mm.[3]

The effect of age.—Fig. 1 and Table III show how the counts varied with age. As for males, each result is an average for 5–15 insects.

For the first four days there was little variation in the blood-cell count. It was approximately 6,000 cells/mm.^{3} There was then an erratic rise to rather over 12,000 cells per c.mm., the values being consistently below those for males.

When the cell count is plotted against weight (fig. 5) it is found that the relationship is not like that for males. In females the weight continued to rise for over three weeks (fig. 6) instead of rather less than two, while in both cases

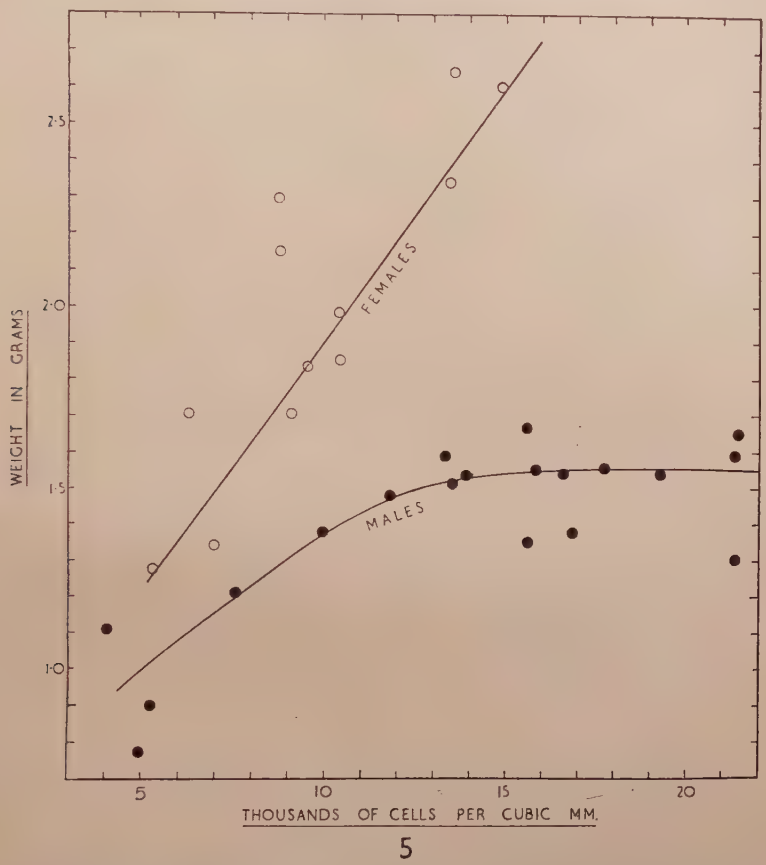

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Fig. 5.—The relation between weight and cell count in adult males (closed circles) and females (open circles). The correlation is simple for females, apparently because growth in weight and increase in cell-count stop at about the same time; in males the increase in cell count continues after growth has stopped.

the cell count rose for about the first three weeks. Consequently there was a wide range of cell count for a constant (maximal) weight in males, but a relatively constant increase of weight and cell count together in females (fig. 5).

Effect of the stage of maturity.—With the help of Mr. J. Phipps, all the females, after sufficient blood had been removed to make a cell count, were classified

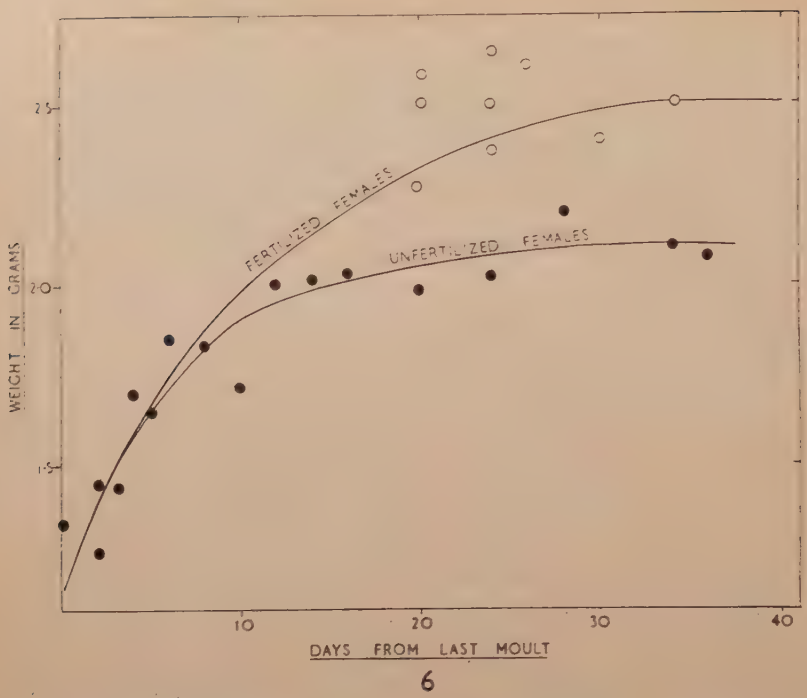

Fig. 6.—Growth in weight of female locusts, showing the effect of copulation.

Table III.—*Blood-Cell Counts and Weights of Adult Females in Relation to Age.*

Days old.	Count.	Weight. (gm.).
Newly emerged	6,044	1·343
1–2	5,500	1·27
3–4	6,318	1·7
5–6	10,408	1·858
7–8	9,534	1·834
9–10	9,155	1·7
11–12	8,825	2·15
13–14	11,873	2·216
15–16	8,878	2·3
17–18	13,133	2·179
19–20	10,441	1·968
21–22	12,800	2·35
23–24	14,445	2·35
25–26	14,760	2·6
27–28	12,200	2·2
29–30	10,800	2·4
31–32	9,600	2·11
60–70	9,445	2·2

according to the stage of their egg development (Phipps, 1950). They were divided into four groups:

Group I: Ovarioles small and white.
,, II: Lowest egg larger and yellow.
,, III: Ripe eggs in ovarioles, no eggs in oviduct.
,, IV: Eggs in oviduct.

The average blood-cell count for each group is shown in Table IV. It can be seen that there was a rise between Groups I and II. Between Groups II and III there was no rise in the cell count, but a further rise occurred between Groups III and IV.

Ten females removed from the cage in the act of oviposition gave an average count of 17,290. This increase over the average count of the female adults is statistically significant.

TABLE IV.

Group.	Age.	Weight.	Count.
I	9 days	1·54 gm.	7,162
II	11 ,,	1·83 ,,	9,857
III	16 ,,	2·22 ,,	9,485
IV	22 ,,	2·45 ,,	12,375

DISCUSSION.

Examination of the results of the 320 blood counts reveals many interesting facts.

If they are compared with those of Tauber & Yeager (1935) the first striking feature one notices is the persistency of the several peaks in both sets of results, even though the actual figures obtained and the number of counts made are different. It is suggested by Tauber & Yeager (1935) that the trimodality is at least partially caused by certain physiological and pathological conditions, such as ecdysis, oviposition and parasitization. If the results presented in this paper are examined it will be seen that the suggestions of the American workers are substantiated. It is possible to divide the counts in the nymphal instars into two groups:

(1) A group for newly moulted animals of any instar.
(2) A group for older insects—those approaching ecdysis.

A third group of results is also present which is entirely due to the relatively high counts obtained in the third instar. In this the count rises to over 10,000 cells/mm.^{3} The conclusion can be drawn that in this instar great metabolic changes, as exemplified by the changing of the position of the wings and their expansion, caused great increases in the number of phagocytic cells. Roonwal (1940) has shown the importance of the third instar in the ACRIDIDAE. The blood-cell counts of the present work give a further physiological indication of its importance. Analysis of both male and female adult counts shows an elongated distribution with peaks. This distribution is due to a progressive rise in the count with increasing age, some very high values for old males, and considerable irregularities.

It was thought in the course of this work that the moisture content of the

insect might play a big part in the cell counts. It was noted repeatedly that the blood from newly emerged insects was easy to extract and less viscous than that obtained from older animals, and the amount of blood freely obtainable decreased markedly with the age of the animal. This was especially the case in the males, which had a very small amount of blood of high viscosity. From the results of the present investigation it seems possible that the fall in percentage water content which takes place in the first 12 days of adult life is one factor which contributes to the apparent increase in cell counts.

It was also thought that the decrease in cell count after ecdysis might be due to a change in the water content. Since the low cell counts after ecdysis were obtained with insects that had not fed (i.e. they were still hardening their cuticles during suspension from the twigs) there could be no increase of water through feeding. The change could, therefore, be brought about only by an adjustment of the distribution of water in the animal.

It is at any rate evident that when blood was readily obtainable the cell count was low, so that some considerable part in the variation in the count was due to variation in fluid in the blood rather than in the total number of blood cells. It is puzzling, however, to find a considerably greater amount of freely available blood *after* the animal had expanded after shedding its old skin. It is very desirable that a method of estimating blood volume of insects should be designed; only with such estimates can these results be more fully interpreted.

Acknowledgments.

I should like to record my gratitude to Professor J. W. Munro, in whose department at Imperial College, London, the work was done during my tenure of an Agricultural Research Council scholarship; to Dr. O. W. Richards and Dr. G. Fraenkel, of that department, for their encouragement and guidance; and to Dr. B. P. Uvarov and Dr. D. L. Gunn, of the Anti-Locust Research Centre, for criticism and advice.

Summary.

(1) Blood-cell counts have been made on blood samples from 320 locusts.

(2) In nymphs the average count was about 7,000 cells per c.mm., with no significant differences between the sexes.

(3) There was a sharp fall in the count at each moult and a rise during each instar.

(4) In the third instar there was a significantly higher count than in the other instars.

(5) The average count for adults was higher than for nymphs at about 9,000 for females and 11,500 for males, rising from about 6,000 in both sexes at emergence to much higher but fluctuating values during the first three weeks of adult life.

(6) These changes are partly due to changes in blood volume, but how far there are also changes in cell numbers cannot be determined until a method is available of estimating blood volume.

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Book Notice.

The Nearctic Leafhoppers (*Homoptera* : *Cicadellidae*). *A generic classification and check list.* By Paul Wilson Oman. 8vo. Entomological Society of Washington, Memoir No. 3, 1949. Pp. 253, 44 pls. Price $7.00 (Members $6.00).

Essentially a key to genera, with a description of each species. There is a discussion of the classification, and a historical account of previous work. A section on bionomics covers life-histories, disease transmission, parasitism and distribution.

The forty-four plates probably average more than a dozen figures each, chiefly of heads and wings, with a few figures of genitalia. There is a long index to trivial names, and a separate index to names of supraspecific category.

NOTES ON A MIGRATORY FLIGHT OF *URANIA FULGENS* WALKER (URANIIDAE) ON THE ISTHMUS OF PANAMA, CENTRAL AMERICA.

By Paul A. Woke.

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The following account is submitted as a contribution to the meagre information on insect migration. On August 11th, 1942, I found a specimen of a day-flying moth, *Urania fulgens*, on the road paralleling the west bank of the Panama Canal opposite Balboa. On the following day I noticed several similar moths in flight in the same locality. During the next two days greatly increased numbers appeared, all pressing in one direction. A mass movement obviously was in progress. The migrants flew steadily on an easterly course, close to the ground, seldom rising higher than about 2 ft. except to pass over, rather than around, such obstructions in their course as bushes, trees and buildings. They appeared never to linger nor to alight.

About five o'clock in the evening of 14th August I counted 60 moths in 20 seconds passing on a 100-ft. front. On the mornings of the 17th and 18th (sunrise at 6.12, sky clear) none were seen in flight before six o'clock. Five one-minute counts of migrants in flight passing on a 50-ft. front between 6.05 and 6.10 gave an average of 3 ; between 6.30 and 7.00, 20 and 47 ; between 7.00 and 7.30, 73 ; and shortly after 8.10, 46. The numbers in flight, after increasing to approximately 85 to 100 per minute on a 50-ft. front, appeared to remain fairly constant at this level throughout the day until after sunset (6.35), although the numbers during the mid-portion of the day may have been somewhat less, and they frequently came over in waves.

The rate of flight continued on a high level for several more days. However, on 27th August, at 6.45 a.m., only 12 were counted in one minute, and on 28th August, at 7.15 a.m., 5 were counted in 2 minutes. The numbers were dropping rapidly, but nearly a month later, on 24th September, at about 6.30 a.m., an average of 5 per minute were counted in five one-minute counts.

At the rate observed on 14th August, which was judged to be about average for several daylight hours each day for the several-day period of the heaviest part of the flight, over 500,000 migrants would have passed on a front of one mile each hour. They were reported by several persons to be flying in similar numbers throughout the area about the Pacific terminus of the canal, and persons travelling by train across the isthmus reported similar numbers throughout this distance. Many millions must have passed over the canal in migratory flight each day.

The prevailing direction of the wind in the vicinity of Balboa during August and September was from the north-west, with an average hourly velocity during August of 4·6 miles per hour, and during September of 4·9 miles per hour. The mean temperature was 78·8° F. (range 71° to 91°) ; 5·40 inches of rain fell during August (1·98 inches on 15th August) and 8·11 inches during September.

On 15th August a light rain began near 5.00 p.m., increasing within fifteen minutes to a heavy downpour. The migrants had been in flight in usual numbers before the start of the rain. During the earlier, lighter part of the rain they continued in flight, apparently little affected in their ability to fly

and to stay on course. As the rain increased in intensity the numbers of moths in flight diminished rapidly, but those in flight appeared little handicapped. None were seen during the height of the downpour, and only a scattered few during and between the irregular light showers which followed.

Appearance in usual numbers was delayed on the morning of 16th August until a heavy fog lifted.

Neither the origin nor the destination of the flight was learned. The three specimens brought to the United States were determined by Dr. Austin H. Clark, Curator, Division of Echinoderms, as *Urania fulgens*, and deposited in the collection of lepidoptera, United States National Museum, Washington 25, D.C. All individuals seen close up in flight resembled the three captured specimens, but no other evidence is available to indicate whether or not the flight might have involved other species.

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Williams, C. B., 1937, The Migrations of Day-flying Moths of the Genus *Urania* in Tropical America, *Proc. R. ent. Soc. Lond.* (A) **12** : 141–147.

Book Notices.

Malaria and its Control in Bombay State. By D. K. Viswanathan. 8vo. Published by the Author, Connaught House, Poona 1, 1950. Pp. 263. 22 figs. Price Sh. 15 or $3.

An account of the organization and work of the Bombay State Malaria Organization, founded in 1942. Because of the effectiveness of DDT as an insecticide, the author divides the review of the work into pre-DDT and post-DDT periods. A number of particular problems relevant to the two periods are discussed, including surveys of particular areas and general matters of technique and efficacy of control measures.

Following this general review the control of malaria in Greater Poona is given as an example of Urban Malaria Control, and a section of 67 pages is given up to malaria surveys of the State, district by district. The last section deals with plans and aspirations, and includes an analysis in some detail of the present condition of surveys, controls and costs of the campaign.

The Mayflies of Florida. By Lewis Berner. 8vo. Gainesville, Florida (University of Florida Press), 1950. Pp. viii + 267. 24 pls., 88 figs., 19 maps. Price $5.50.

The first 18 pages consist of a general introduction to the Ephemeroptera, an account of the characters used in classification, and a history of previous work on the Mayflies of Florida. Then follow a comparison of Florida mayflies with the Northern fauna and an appreciation of the factors affecting the ecology, life history and abundance, dispersal and geographical distribution. The habitats of the mayflies of Florida are analysed at some length.

The systematic section begins on p. 43 with a key and check list of species. Following this, and occupying the last part of the work is a detailed account, species by species, with the headings : Taxonomy, Distribution, Ecology, Season, Habits and Life History, and, finally, Locality Records.

There is a full bibliography.

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——, 1936, New species of COCCIDAE. *Trans. R. ent. Soc. Lond.* **84** : 901–936.

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